

1976

Zooplankton of the Gulf of Mexico: Distribution of Displacement Volume, Occurrence of Systematic Groups, Abundance and Diversity Among Copepods.

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ZOOPLANKTON OF THE GULF OF MEXICO:
DISTRIBUTION OF DISPLACEMENT VOLUME,
OCCURRENCE OF SYSTEMATIC GROUPS,
ABUNDANCE AND DIVERSITY AMONG COPEPODS.

The Louisiana State University and
Agricultural and Mechanical College,
Ph.D., 1976
Zoology

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ZOOPLANKTON OF THE GULF OF MEXICO: DISTRIBUTION
OF DISPLACEMENT VOLUME, OCCURRENCE OF SYSTEMATIC GROUPS,
ABUNDANCE AND DIVERSITY AMONG COPEPODS

A Dissertation

Presented to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Zoology and Physiology

by

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August, 1976

ACKNOWLEDGMENTS

I wish to thank the members of my guidance committee, Drs. William B. Stickle, J. M. Fitzsimons, Walter J. Harman of the Department of Zoology and Physiology; Dr. John Day of the Department of Marine Science; and especially Dr. Taisoo Park, Department of Oceanography, Texas A & M University, for their assistance and constructive criticism throughout the course of this study. Dr. Park and members of his staff also assisted me in the identification of some copepods. I would like to thank Dr. William Richards of the National Marine Fisheries Service, Southeastern Fisheries Center, Miami, for assistance in making available the samples used in this study. Dr. Prentiss Schilling and Mr. David Blouin, Department of Experimental Statistics, provided invaluable assistance in the analyses of data.

TABLE OF CONTENTS

	Page
ACKNOWLEDGMENTS	ii
LIST OF TABLES.	v
LIST OF FIGURES	vii
ABSTRACT.	viii
PART I: DISTRIBUTION OF ZOOPLANKTON DISPLACEMENT VOLUMES IN THE GULF OF MEXICO AND OCCURRENCE OF SYSTEMATIC GROUPS	1
INTRODUCTION	2
MATERIALS AND METHODS.	4
RESULTS.	10
Hydrographic Data	10
Displacement Volume	12
Taxonomic Groups.	19
DISCUSSION	22
SUMMARY.	29
LITERATURE CITED	31
PART II: ABUNDANCE AND DIVERSITY AMONG COPEPODS IN THE GULF OF MEXICO.	34
INTRODUCTION	35
MATERIALS AND METHODS.	38
RESULTS AND DISCUSSION	40
Limitations of the Data	40
Abundance of Copepods	42
Systematic Account.	61

	Page
Geographic Variation.	72
Diel Variation.	74
The Ten Most Abundant Species	76
Population Parameters	80
SUMMARY.	86
LITERATURE CITED	88
VITA	93

LIST OF TABLES

Table	Page
1. Adjusted mean values of salinity and temperature arranged by location and time of measurement	11
2. Adjusted mean zooplankton volumes for three areas by time of collection.	17
3. Relationship between drained displacement volume and displacement volume measured with the mercury immersion method for ten plankton samples randomly selected from those examined.	18
4. Summary of occurrence of selected taxa in 180 samples examined from the Gulf of Mexico (Percent composition of samples)	20
5. Mean values (percent) for occurrence of observed taxa in day and night collected plankton samples.	21
6. Zooplankton volumes from various tropical and temperate localities for comparable months of the year	23
7. Mean values (individuals/100 m ³) for calanoid and non-calanoid copepods in each area, and day and night means for samples collected in water exceeding 200 m in depth	43
8. List of species identified from all samples examined together with their mean abundance (individuals/100 m ³) for the entire study, and each area for samples collected during daylight hours and at night. A + means that a species was present with an abundance of less than one individual/100 m ³ , and an asterisk (*) means that a species was identified from a sample other than those analyzed in detail	50
9. Mean abundance (individuals/100 m ³) in each area of those copepod species having statistically significant differences among areas. Group A was more abundant in shelf waters; Group B was more abundant in slope or oceanic waters	73

Table

Page

10. Mean abundance (individuals/100 m³) of those copepod species having significantly different abundances between samples collected during daylight hours and at night. Group A was more abundant during daylight hours, group B was more abundant at night 75
11. The ten most abundant species for the overall study, and each area together with the mean abundance of each species (individuals/100 m³) 77
12. Mean values of several population parameters calculated for each area. Natural logarithms have been used in all calculations requiring log functions. 81

LIST OF FIGURES

Figure	Page
1. Stations occupied by R/V OREGON II during August 1971 on cruise 7129. Open circles indicate stations occupied during daylight hours, and solid circles indicate stations occupied at night.	5
2. Stations occupied by R/V TURSIOPS during August, 1971 on cruise 7121. Open circles indicate stations occupied during daylight hours, and solid circles indicate stations occupied at night.	6
3. Stations occupied by R/V OREGON II during August, 1971 on cruise 7131. Open circles indicate stations occupied during daylight hours, and solid circles indicate stations occupied at night.	7
4. Zooplankton displacement volumes during August, 1971 on R/V OREGON II cruise 7129.	13
5. Zooplankton displacement volumes during August, 1971 on R/V TURSIOPS cruise 7121	14
6. Zooplankton displacement volumes during August, 1971 on R/V OREGON II cruise 7131.	15
7. Abundance of calanoid copepods in August, 1971 on R/V OREGON II cruise 7129	44
8. Abundance of calanoid copepods in August, 1971 on R/V TURSIOPS cruise 7121.	45
9. Abundance of calanoid copepods in August, 1971 on R/V OREGON II cruise 7131	46
10. Abundance of non-calanoid copepods during August, 1971 on R/V OREGON II cruise 7129.	47
11. Abundance of non-calanoid copepods during August, 1971 on R/V TURSIOPS cruise 7121	48
12. Abundance of non-calanoid copepods during August, 1971 on R/V OREGON II cruise 7131.	49

ABSTRACT

Displacement volume and abundance of major taxa were determined for 180 zooplankton samples collected during August and November in the Gulf of Mexico and adjacent waters of the Caribbean Sea by the National Marine Fisheries Service. Oblique tows from the surface down to 200 m depth were made using 60 cm Bongo Net samplers equipped with a net having a mesh aperture size of 0.333 mm.

Displacement volume was measured by the mercury immersion method. Mean zooplankton displacement volume for all samples was 0.053 cc/m^3 . For the three areas into which the samples were grouped, mean displacement volumes were: continental shelf waters, 0.111 cc/m^3 ; continental slope waters, 0.033 cc/m^3 ; and oceanic waters, 0.025 cc/m^3 . In waters exceeding 200 m in depth, there was a significant difference in displacement volume between samples collected during daylight hours and those collected at night. Displacement volumes were 1.4 and 2.3 times greater at night over the continental slope and in oceanic waters respectively. Zooplankton volumes are high in areas near the mouth of the Mississippi River, suggesting that the river markedly affects the standing crop of zooplankton in waters of the northern Gulf.

Copepods were the most abundant group of zooplankton comprising 62.85 percent of the samples. Ostracods comprised 11.60 percent of the samples followed by chaetognaths, 11.02 percent and other crustaceans, 7.72 percent. Other organisms made up less than 10

percent of the zooplankton. No significant difference in relative abundance among areas was present. Significant diel variations in relative abundance were present for copepods, chaetognaths, mollusks and tunicates.

The mean abundance of calanoid copepods was 4692 individuals/100 m³. They were most abundant in waters over the continental shelf where their mean abundance was 10809 individuals/100 m³. They were less abundant in continental slope waters, where the mean was 2175 individuals/100 m³; and they were least abundant in oceanic waters, where the mean abundance was 1680 individuals/100 m³. The mean abundance for non-calanoid copepods was 469 individuals/100 m³. Like calanoids, non-calanoids were most abundant in shelf waters, less abundant in slope waters and least abundant in oceanic waters. There was much variability, however, and this observed difference in abundance was not statistically significant.

One hundred one species of copepods were identified from the samples. Statistically significant differences in abundance were detected for 31 species. Sixteen species were more abundant in shelf waters and 15 species were more abundant in slope or oceanic waters. Diel variation in abundance was detected for 16 species. Eight species were more abundant during daylight hours and seven species were more abundant at night. The relative abundance of the most abundant species was different in the different areas.

Species diversity was greatest in oceanic waters, lower in slope waters and lowest in waters over the continental shelf. Species

richness was greatest in slope and oceanic waters and about one-third less in waters over the continental shelf. Species evenness was greatest in oceanic waters, intermediate in slope waters and lowest in shelf waters.

PART I

**DISTRIBUTION OF DISPLACEMENT VOLUMES IN THE
GULF OF MEXICO AND OCCURRENCE OF SYSTEMATIC GROUPS**

INTRODUCTION

Assessment of the potential of a region for commercial fishing purposes is, to an extent, based on the quantity and composition of zooplankton present. Few studies have been made of the biomass and composition of zooplankton from the Gulf of Mexico, especially in oceanic areas. Taxonomic studies, or studies of a few groups of organisms comprise much of the rather meager literature concerning this body of water.

Although some quantitative studies have been undertaken, most deal with coastal areas and embayments and are of limited geographical scope. Dragovich (1963) enumerated groups of zooplankton present in the coastal waters around Naples, Florida. Kelly and Dragovich (1967) examined volume and composition of zooplankton in Tampa Bay, Florida and adjacent waters of the Gulf of Mexico on a semiquantitative basis. Hopkins (1966) examined zooplankton biomass and composition in the St. Andrews Bay system of Florida. Perry and Christmas (1973) reported zooplankton volumes from Mississippi Sound and the Biloxi Bay estuary in the state of Mississippi. Cuzon du Rest (1963) determined numbers of several groups of zooplankters from estuarine lakes in southeastern Louisiana. Mulkana (1968) examined the biomass and composition of zooplankton in Barataria Bay and adjacent estuaries. Gillespie (1971) determined volume of zooplankton and numerical abundance of several taxa from six coastal areas of Louisiana on a

seasonal basis. Drummond and Stein (1954) conducted quantitative studies on the biomass of zooplankton over the continental shelf off Texas and discussed the differences which they found.

Studies encompassing wider geographic areas, or waters further from the coast are few in number. Austin and Jones (In Press) reported zooplankton volumes from an offshore area over the continental shelf in the northeastern Gulf of Mexico. De La Cruz (1971) has reported zooplankton biomass from waters over the Campeche Bank north of Yucatan. Fleminger (1956) examined nearly 200 plankton samples from all parts of the Gulf of Mexico and reported the total volume of each nonquantitative sample as part of an appendix to a taxonomic study. In 1964 the Soviet Union and Cuba jointly began extensive studies in the Gulf of Mexico. These studies have included determinations of zooplankton biomass which has been briefly summarized by Bogdanov *et al.* (1968).

The present study is part of a more extensive examination of the zooplankton of the Gulf of Mexico which shall include studies on the abundance and distribution of copepods. In this study the displacement volumes of plankton samples representing a large area of the Gulf of Mexico are reported together with data on the relative abundance of major taxonomic units which comprise the zooplankton. An attempt is made to correlate composition, biomass, location and time of day that the samples were collected.

MATERIALS AND METHODS

Zooplankton samples collected from 180 stations in the Gulf of Mexico and adjacent Caribbean Sea were obtained from the National Marine Fisheries Service (NMFS), Southeastern Fisheries Center, Miami. These were collected on three cruises which were part of the Marine Resources Monitoring Assessment and Prediction (MARMAP) and Exploratory Gulf of Mexico (EGMEX) programs. Samples were collected during two cruises made simultaneously during August, 1971 by the research vessels TURSIOPS and OREGON II. A third cruise during November, 1971 by the vessel OREGON II provided additional samples.

Eighty-five samples were collected by the OREGON II from stations on four east-west transects spanning the Gulf of Mexico north of latitude 24°N on NMFS cruise 7129 (Figure 1). Forty-seven samples were collected by the TURSIOPS during NMFS cruise 7121 in the northeastern Gulf (Figure 2). The remaining 48 samples were collected by the OREGON II on NMFS cruise 7131 in the southeastern Gulf and adjacent Caribbean Sea east of Yucaton (Figure 3).

All samples examined were collected using 60 cm (mouth diameter) Bongo Net samplers (Ocean Instruments Co., San Diego, Ca.). The sampler was equipped with nets having 0.333 mm and 0.505 mm mesh apertures. A Tsurumi Precision Instrument Company (TSK) Flowmeter was centrally mounted in the mouth of the side of the

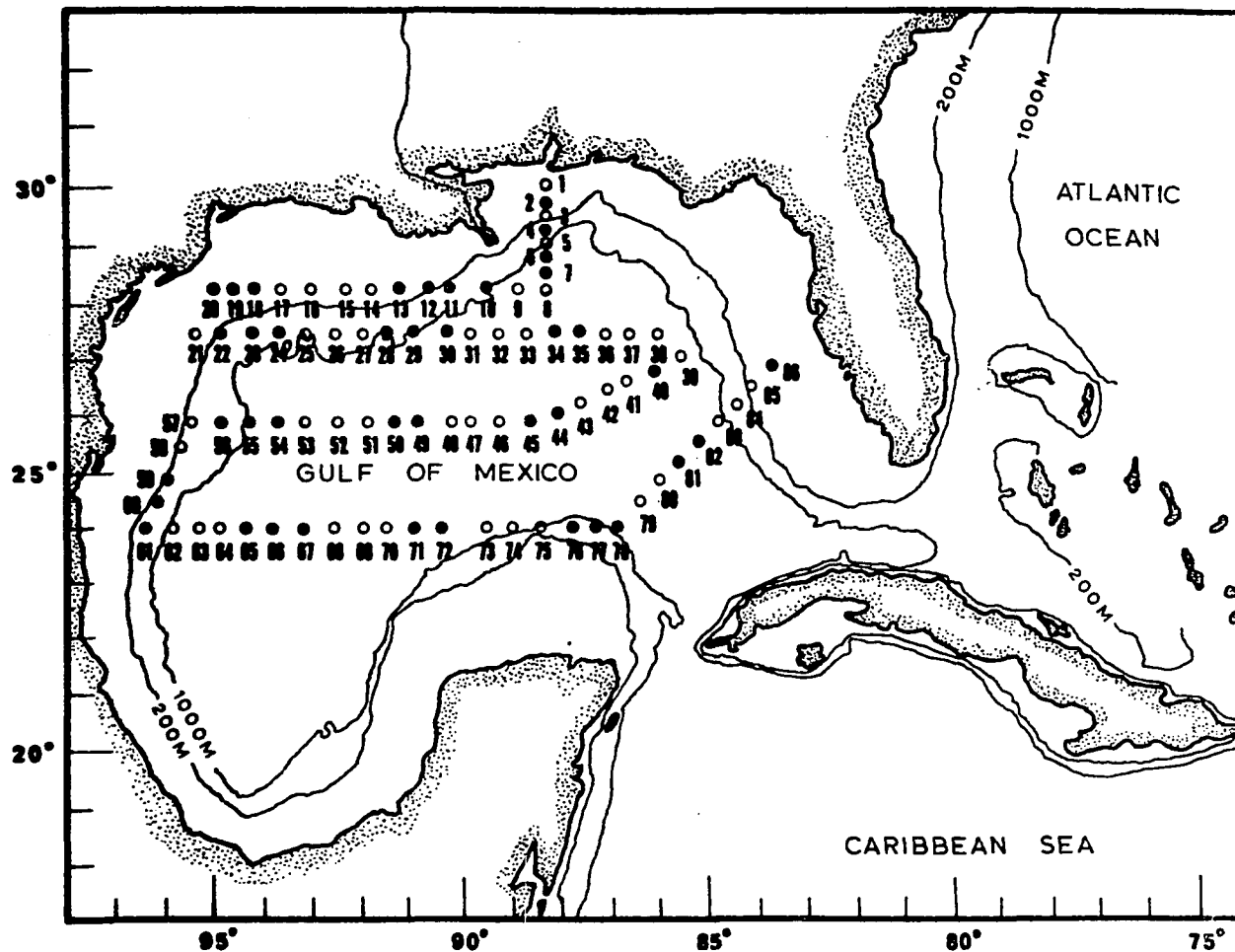


Figure 1. Stations occupied by R/V OREGON II during August, 1971 on cruise 7129. Open circles indicate stations occupied during daylight hours, and solid circles indicate stations occupied at night.

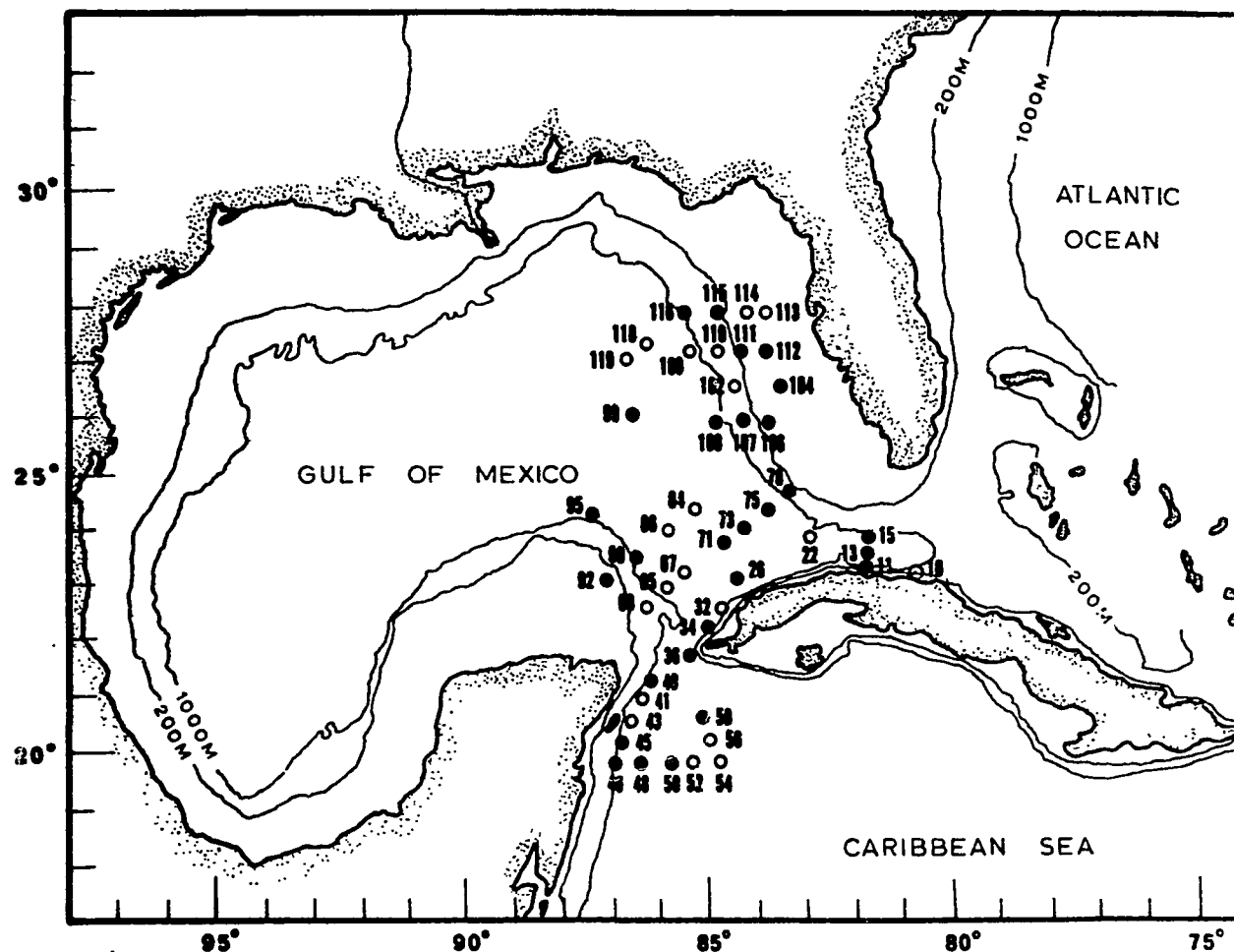


Figure 3. Stations occupied by R/V OREGON II during November, 1971 on cruise 7131. Open circles indicate stations occupied during daylight hours, and solid circles indicate stations occupied at night.

sampler equipped with the 0.505 mm mesh net. Since only samples collected by the 0.333 mm mesh net were examined, it was necessary to evaluate the filtration characteristics of the two nets. The nets differed only in mesh size and, therefore, differ primarily in their porosity (Tranter and Smith, 1968). Based on data presented by Tranter and Smith (1968), the 0.505 mm mesh net should have a porosity approximately 10.4 percent greater than the 0.333 mm mesh net. Data were obtained from the NMFS for 65 plankton tows made using the gear described above with the exception that a flowmeter was mounted in the mouth of each net. The amount of water filtered by each net could then be determined when otherwise identical tows were made. Statistical analysis showed that there was no significant difference in the volume of water filtered by the nets of different mesh size (paired t-test $p < 0.0001$).

Plankton samples were collected by means of oblique tows made from the surface down to about 200 m depth (depth permitting). Maximum depth sampled was determined by means of a bathykymograph (BKG). Actual maximum depth sampled ranged from two to 265 m. Volume of water filtered ranged from 17.27 to 1040.46 m³.

Samples were immediately preserved in five percent formalin in sea water buffered with marble chips, sent to the Southeastern Fisheries Center, Miami, Florida, and later shipped to Louisiana State University for analyses.

Displacement volume for each plankton sample was determined by the mercury immersion method of Yentsch and Hebard (1957) with the single modification being use of vacuum to remove interstitial

water from the sample. Sargassum, other large pieces of plant material and animals exceeding 2 cm in greatest dimension were removed from the samples prior to determination of displacement volume and subsampling.

Subsampling was accomplished by adding sufficient fluid to a sample while in a beaker to bring the fluid level to 1000 ml. The sample was then agitated so that all organisms were evenly dispersed and 10 ml aliquots removed with a Stempel pipette until a manageable subsample was obtained. Normally from one to five percent of each sample was examined and the individuals counted and tabulated.

Statistical analyses, including analysis of variance and multiple correlation, were performed using the Statistical Analysis System.

RESULTS

Hydrographic Data

Water salinity was measured at 84 stations where plankton samples were collected. The mean surface salinity for these stations was 34.98‰. There were significant differences in salinity with regard to both location and time of day. Mean values, adjusted for equal sample size, for each of the three areas examined were: continental shelf, 34.49‰; continental slope, 34.71‰; oceanic, 35.62‰. Adjusted mean salinity for stations occupied during daylight hours was 34.50‰ and for stations occupied during night hours was 35.39‰. Mean values of salinity measured during day and night in each area are given in Table 1.

Surface temperature was measured at 151 stations where zooplankton was collected. The mean temperature for these stations was 28.88°C. Mean temperature for shelf, slope and oceanic waters were: 28.94, 28.69 and 28.89°C respectively. There was no significant difference in temperature among the three areas studied. The mean surface temperature for stations occupied during daylight hours was 29.24°C and that for stations occupied during night hours was 28.43°C. This difference was found to be statistically significant. Mean temperatures for day and night at each of the three areas studied are given in Table 1.

Examination of depth profiles for both temperature and salinity indicates that the range is greater at a single station

Table 1. Adjusted mean values of salinity and temperature arranged by location and time of measurement.

Location		Salinity (‰)	n	Temperature (°C)	n
Continental Shelf	Day	35.42	20	29.09	23
	Night	34.46	15	28.65	21
Continental Slope	Day	34.24	8	28.63	15
	Night	35.64	8	28.85	15
Oceanic	Day	35.16	16	28.66	41
	Night	34.72	17	29.03	36

within the upper 200 m where plankton was collected than it was for the surface values of temperature and salinity for all stations. Although this severely limits the usefulness of this data, it is included since it is related to the zooplankton in at least indirect ways.

Displacement Volume

The mean displacement volume for all zooplankton samples was 0.053 cc/m^3 with a range from 0.001 to 0.409 cc/m^3 . The minimum value was recorded from station 78 and the maximum at station one, both on cruise 7129. Mean volumes for the three groups of samples examined were: Cruise 7121, 0.107 cc/m^3 ; Cruise 7129, 0.043 cc/m^3 ; Cruise 7131, 0.020 cc/m^3 . The areal distribution of displacement volumes is shown on Figures 4-6.

Zooplankton displacement volumes were related to several factors. When grouped by collection area there was a highly significant positive correlation between location and volume. Adjusted mean volumes by area were: continental shelf, 0.111 cc/m^3 ; continental slope, 0.033 cc/m^3 ; and oceanic waters, 0.025 cc/m^3 .

When all of the samples were considered, there was no significant difference in zooplankton volumes of samples collected during daylight hours and those collected at night. However, the sampling technique was such that virtually the entire water column was sampled over the continental shelf. This eliminated the possibility of any diel biomass variation that might be due to vertical migration of organisms. Mean volumes, adjusted for equal sample size, for samples

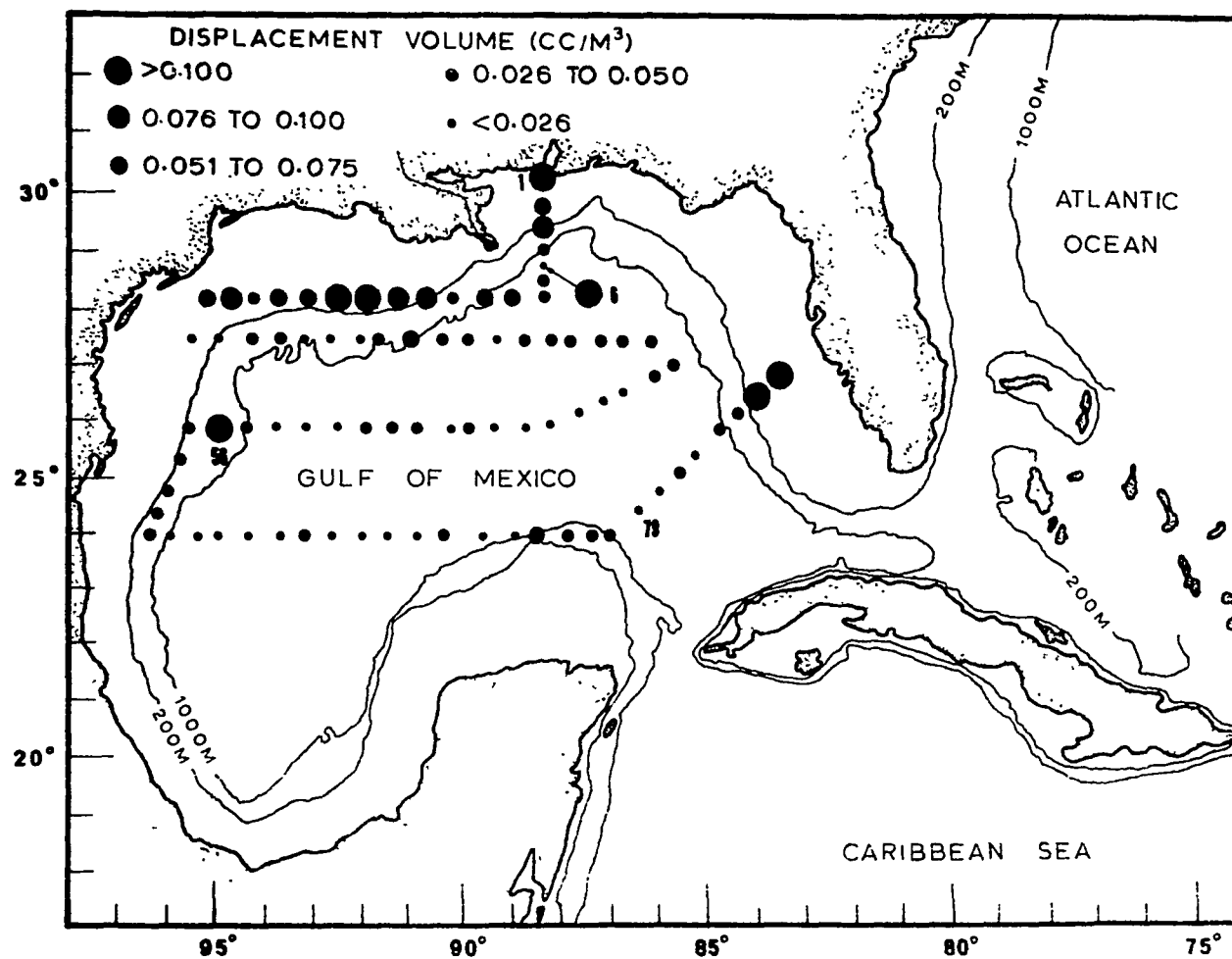


Figure 4. Zooplankton displacement volumes during August 1971 on P/V OREGON, cruise 7129.

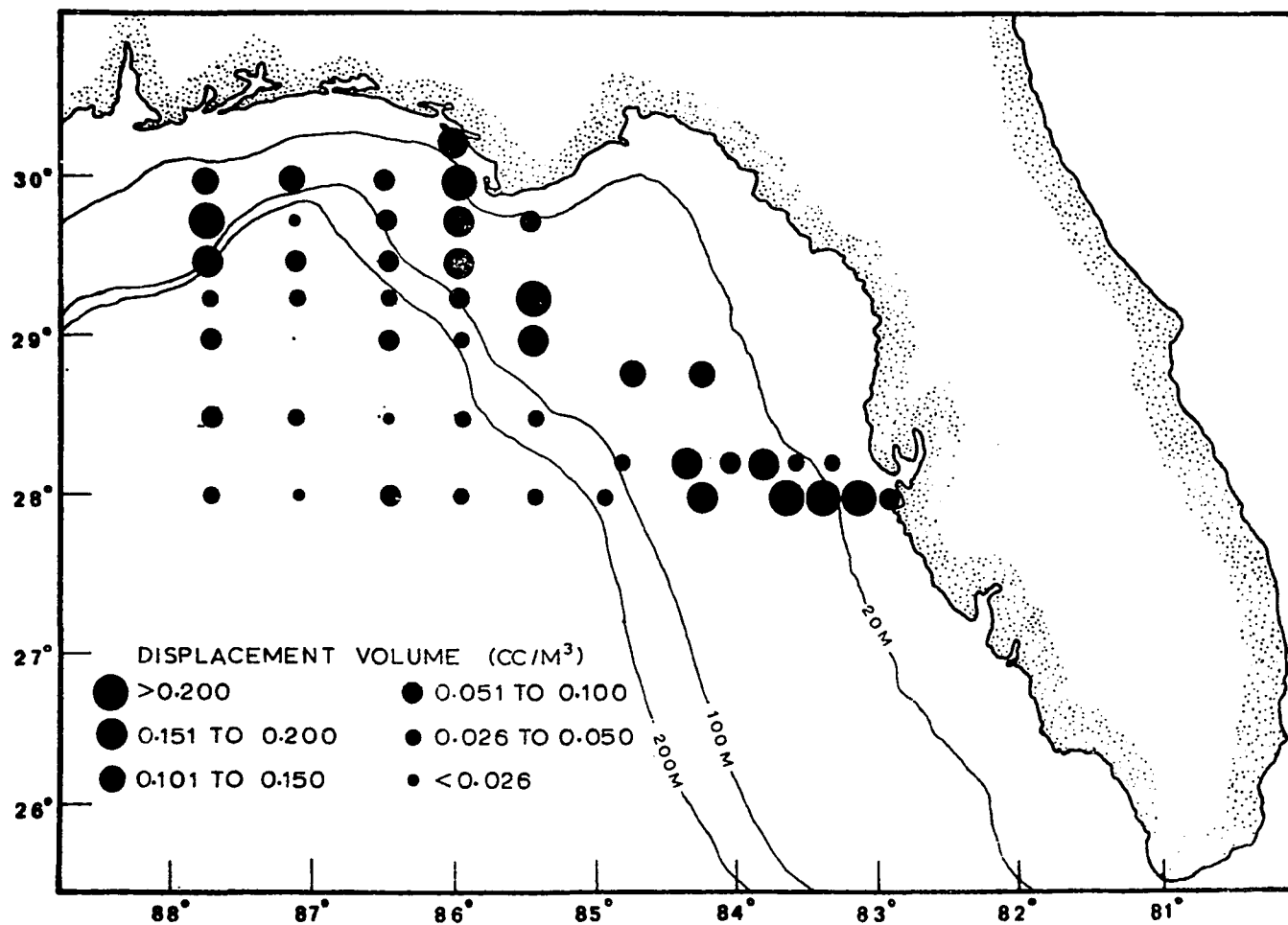


Figure 5. Zooplankton displacement volumes during August 1971 on R/V TURSIOPS cruise 7121.

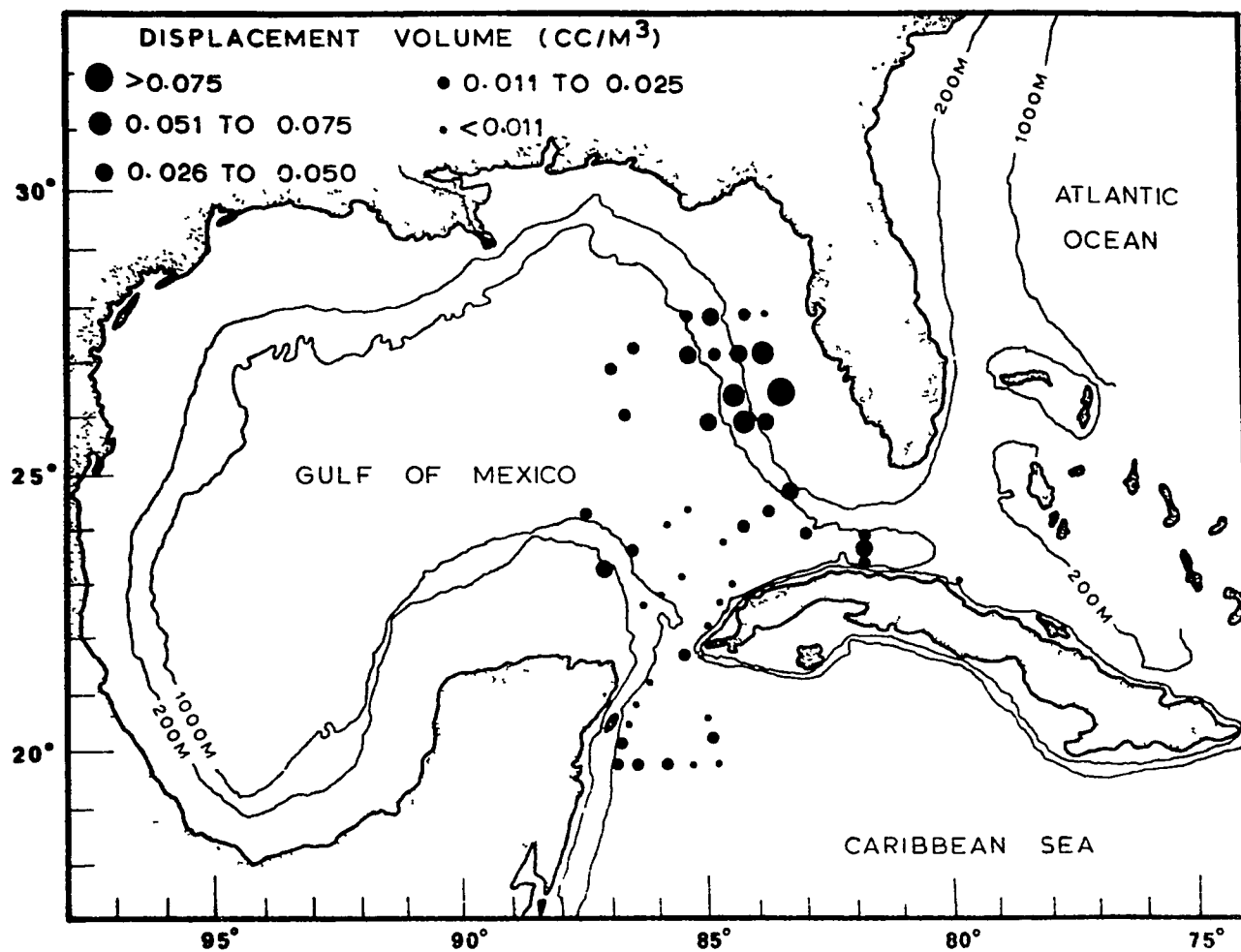


Figure 6. Zooplankton displacement volumes during November 1971 on R/V OREGON II cruise 7131.

collected during daylight hours and at night were 0.052 cc/m^3 and 0.069 cc/m^3 respectively. When all samples collected over the continental shelf were deleted from analysis, samples collected at night had a significantly greater ($p < 0.05$) average displacement volume than did those collected during the day. Table 2 shows the mean plankton volumes obtained for shelf, slope and oceanic waters during daylight hours and at night.

Since zooplankton volume has been measured and reported in several different ways, it was necessary to evaluate the relationship between some of these methods. St. John (1958) has compared the displacement and settling volumes of zooplankton samples and concluded that settlement volumes could be converted to displacement volumes by dividing by four. However, the relationship between drained plankton volumes measured by the displacement method and displacement volume measured by the mercury immersion method has not been thoroughly investigated. In order that the results of this study might more meaningfully be compared to results of other studies, this relationship was evaluated. Ten plankton samples were randomly selected and drained plankton volume determined by the displacement method of Ahlstrom and Thraillkill (1963). These volumes were compared to the volumes obtained by the mercury immersion method used in the present study. The results of this comparison are shown in Table 3. The average ratio of drained displacement volume to volume determined by the mercury immersion method was found to be 1.52 (Range: 1.23-1.95).

Table 2. Adjusted mean zooplankton displacement volumes for three areas by time of collection.

Location	Time	Volume (cc/m ³)	n
Continental Shelf	Day	0.074	26
	Night	0.039	28
Continental Slope	Day	0.048	21
	Night	0.066	17
Oceanic	Day	0.028	45
	Night	0.065	44

Table 3. Relationship between drained displacement volume and displacement volume measured with the mercury immersion method for ten plankton samples randomly selected from those examined.

<i>Cruise</i>	Sample	Drained Volume (cc)	Hg immersion	Ratio
7129	38	34.2	25.16	1.36
	43	10.8	6.61	1.63
	57	25.7	18.76	1.37
	60	23.1	17.26	1.34
	62	22.6	11.61	1.95
	75	52.2	35.62	1.47
	86	38.5	24.31	1.58
7121	109	7.0	3.66	1.91
	117	16.6	13.46	1.23
	118	29.5	21.56	<u>1.37</u>
Correlation coefficient $r=0.979$		Mean		1.52
f value 184.899		Standard deviation		0.245
Probability $p \leq 0.0001$		Standard error		0.078

Taxonomic Groups

Calanoid copepods numerically dominated most plankton samples accounting for an average of 52.01 percent of all samples. Non-calanoid copepods, ostracods and chaetognaths each contributed more than 10 percent, on the average, to the total number of plankters present. Collectively these four groups comprised 85.44 percent of the total number of zooplankters. Ostracods were the only group other than calanoid copepods which ever comprised more than 50 percent of any sample. Mean percentage and range for the ten divisions of zooplankton determined are given in Table 4.

There was no significant difference in composition by group among the three areas into which the samples were divided, although species composition did undoubtedly change. The composition of the zooplankton was different for some groups during the day than at night. Table 5 shows the relationship between time of collection and percentage composition for the zooplankton samples. There was a significant difference ($p < 0.05$) between day and night collections for calanoid copepods and tunicates and a highly significant difference ($p < 0.01$) for non-calanoid copepods, chaetognaths and mollusks.

Table 4. Summary of occurrence of selected taxa in 180 samples examined from the Gulf of Mexico. (Percent composition of samples)

	Mean Value	Minimum	Maximum	Standard Deviation
Calanoid Copepods	52.01	0.04	91.08	15.21
Non-Calanoid Copepods	10.84	0.00	40.55	7.60
Amphipods	1.87	0.00	29.17	4.55
Ostracoda	11.60	0.00	76.40	15.08
Other Crustacea	7.21	0.68	33.33	4.78
Chaetognaths	11.02	0.44	36.96	6.57
Mollusks	1.34	0.00	7.05	1.76
Tunicates	0.80	0.00	38.54	3.68
Fish larvae	0.67	0.00	3.46	0.58
All Others	2.25	0.00	82.31	6.25

Table 5. Mean values (percent) for occurrence of observed taxa in day and night collected plankton samples.

Group	Day	Night
Calanoid copepods	51.49	53.57
Non-Calanoid Copepods	10.32	9.97
Amphipods	1.70	
Ostracods	12.41	12.47
Other crustacea	6.31	8.28
Chaetognaths	10.94	10.39
Mollusks	1.18	1.37
Tunicates	1.30	0.36
Fish larvae	0.57	0.74
All others	2.76	1.73

DISCUSSION

There are several difficulties which arise when attempts are made to compare the biomass of zooplankton determined in this study to that reported from other studies. These primarily result from different methods. During sample collecting such factors as net design, mesh size and method of sampling may differ in individual studies. Length of preservation may affect displacement volume due to shrinkage of the organisms (Ahlstrom and Thraikill, 1963) and different workers may use different laboratory procedures which may introduce variation among studies. Some problems associated with the comparison of plankton volumes from different studies are discussed by St. John (1958).

Comparative data for selected localities in temperate and tropical waters are presented in Table 6. Additional zooplankton volumes have been summarized by St. John (1958) and Cushing (1969). The data in Table 6 have been adjusted by multiplying drained displacement volumes by 0.658 to convert them to values comparable to those yielded by the mercury immersion method.

Plankton volumes from waters over the continental shelf of the Gulf of Mexico were similar to those reported from other coastal areas for equivalent times of the year. Mean volume for shelf waters in the present study was 40 percent less than that reported for inshore waters of the Cape Hatteras region (St. John, 1958); approximately half those reported for inshore waters off the coast of

Table 6. Zooplankton volumes from various tropical and temperate localities for comparable months of the year.

Location	Adjusted Volume (cc/m ³)	Month	Mesh Size (mm)	Reference
Cape Hatteras- Cape Fear	0.184	June	0.363	St. John, 1958
Gulf of Maine	0.027	Summer	0.366	Sherman, 1970
Bermuda	0.18	August	0.363-	Deevey, 1971
	0.16	8 Nov	0.202	"
	0.16	24 Nov		"
Washington & British Columbia	0.011 (inshore) 0.032 (offshore)	July "	0.239	Frolander, 1962 "
California Current	0.106	July	0.55- 0.25	Isaacs, Fleminger and Miller, 1971
Taiwan	0.049-0.066	Annual Means	0.33	Tseng, 1970
Hawaii	0.118 (day) 0.290 (night) 0.165 (day) 0.368 (night)	August August November November	0.656- 0.308	Shomura and Nakamura, 1969
Central Pacific	0.043	Jul-Aug	0.65- 0.31	King and Hida, 1957
Sargasso Sea	0.013	August	0.23	Grice and Hart, 1962
NE Gulf of Mexico	0.256 (surface) 0.349 (15 m) 0.112 (30 m)	Annual Means	0.200	Austin and Jones, In Press
Gulf of Mexico (Present Study)	0.053 (overall) 0.111 (shelf) 0.033 (slope) 0.025 (oceanic)	August and November	0.333	Present Study

Washington and British Columbia by Frolander (1962), and from 1.5 to three times greater than volumes reported by Nakamura (1967) and Shomura and Nakamura (1969) for inshore waters around Oahu, Hawaii. Austin and Jones (In Press) report mean annual volumes 2.5 times as great, 3.5 times as great, and approximately equal to the mean shelf volume of the present study for their mean volumes collected at the surface, 15 m deep, and 30 m deep respectively in the northeastern Gulf of Mexico.

Zooplankton volumes from the waters over the continental slope and oceanic waters were similar to those reported from the Gulf of Maine (Sherman, 1970) and to volumes reported from offshore stations in the northeastern Pacific (Frolander, 1962). The volumes were about half those reported by Tseng (1970) from the waters surrounding Taiwan and from 60 to 70 percent of the volumes reported by King and Hida (1957) from the central Pacific.

Zooplankton volumes obtained in the present study for waters not over the continental shelf were higher than those reported from some low latitude Atlantic waters. Mean volume in the present study was two to three times those reported by Grice and Hart (1962) for the Sargasso Sea and one and one-half to two times as great as volumes reported from around Bermuda by Deevey (1971) for similar times of the year.

The pattern of greater plankton volumes at night is in agreement with other studies. This has generally been attributed to two factors. Vertical movement of zooplankton appears to be the primary reason for greater volumes of plankton in surface waters at night.

Avoidance of nets by plankton during daylight hours has been implicated as a second factor to account for diel variation by Clutter and Anraku (1968).

In the present study the mean volume for night collected samples was 1.38 times greater than that of day collected samples for waters over the continental slope and 2.30 times greater for samples collected in oceanic waters. In waters over the continental shelf, the mean volume was 1.89 times greater for day collected samples than samples collected at night. The lack of greater volumes at night may be explained by the fact that over the continental shelf the entire water column was sampled, and also suggests that avoidance of nets is probably not an important factor in increased volumes during darkness. The mean for samples collected during daylight hours over the continental shelf, despite its large value, is not significantly different from the mean volume collected during hours of darkness. This situation exists because several samples of excessively large volume were collected during daylight hours.

The distribution of zooplankton biomass in the Gulf of Mexico for the samples examined follows closely the pattern generally reported for other geographic areas. The occurrence of samples having large volumes in waters near coastlines is widely known. It has been called the "land-mass effect" and has been discussed by Friedrich (1969). Additional factors which may influence the distribution of zooplankton in the Gulf of Mexico include upwelling and the presence of the Mississippi River. In both cases this is broadly attributable to an increased availability of nutrients locally and results in a high value for the biomass of zooplankton.

Upwelling has been shown to occur in several areas in the Gulf of Mexico at various times of the year and is associated with areas of high productivity and standing stock of zooplankton by Bogdanov *et al.* (1968). The main areas of upwelling for either the summer months or the entire year are located over the continental slope along the west coast of the Florida peninsula and westward to near the mouth of the Mississippi River, an area south of the western half of Louisiana, and an area paralleling the northern coastline of the Yucatan peninsula. Although not subjected to statistical analyses, the samples examined in the present study that were collected in these general areas regularly had greater volumes than samples from surrounding waters where upwelling has not been reported to occur. Austin and Jones (In Press) also suggested that upwelling is of importance as a controlling factor for zooplankton biomass in the waters of the Florida Middle Ground, which is situated near stations 44 and 45 of cruise 7121 of the present study.

The Mississippi River appears to markedly affect the waters of the northern Gulf. Water flowing from the Mississippi River flows westward along the coastline on the surface until it gradually mixes with the waters of the Gulf. Riley (1937) studied phytoplankton and nutrient levels in the vicinity of the mouth of the Mississippi and concluded that the nutrient input by the river contributed greatly to the productivity of the area. The present study and the results of Bogdanov *et al.* (1968) show an area of large zooplankton biomass in the vicinity of the river mouth and westward from it. Depressed surface salinities at these stations suggests that they are under the

influence of freshwater input from rivers discharging into the area, the largest and probably most important of which is the Mississippi River.

Zooplankton in the Gulf of Mexico is similar in composition and relative abundance to that of other tropical and subtropical plankton communities. It should be noted, however, that the present study reports only on systematic groups of zooplankters and not on species within the groups. Even though differences in composition do not exist among the three areas examined, it is entirely possible that the species composition may change significantly. This is something that should be further investigated and the author is presently evaluating the species composition of the copepods for the samples considered here. When completed, the study will hopefully further elucidate some of the relationships within the plankton community of the Gulf of Mexico.

Despite the paucity of data in the literature, several groups tabulated in the present study may be compared to similar studies for other areas. Copepods comprised 62.85 percent of the total zooplankters in the present study as compared to 69.90 percent in the Sargasso Sea (Deevey, 1971), 63.20 percent for Hawaiian waters (Shomura and Nakamura, 1969) and 57 percent for equatorial waters of the central Pacific (King and Demond, 1953). Shomura and Nakamura (1969) separated copepods into calanoid and non-calanoid groups and found respectively 59.8 and 3.4 percent for these groups as compared to 52.0 and 10.8 percent in the present study for the same groups respectively. Chaetognaths, which comprised 11 percent of the present

samples, made up only three percent of the plankton from the Sargasso Sea (Deevey, 1971), five percent of the plankton from around Hawaii (Shomura and Nakamura, 1969), and 12 percent of the plankton from the central Pacific (King and Demond, 1953). Ostracods comprised 11.6 percent of the present samples, made up 7.20 percent of the plankton of the Sargasso Sea (Deevey, 1971) and 2.9 percent of the plankton from Hawaiian waters (Shomura and Nakamura, 1969).

These comparisons show that copepods comprised a large part of the plankton community in the Gulf of Mexico and that these values are very close to those found in other similar areas. The available data for chaetognaths and ostracods, which were both important components of the zooplankton from the Gulf of Mexico, show much variation among different localities and is not easily explained. Sampling technique and analytical procedures may account for some of these discrepancies, others may reflect real geographic differences.

Diel variations were present in calanoid copepods, non-calanoid copepods, chaetognaths, mollusks and tunicates in the present study. Of these, calanoid copepods and mollusks were the only groups found by Nakamura (1967) to exhibit diel variations in relative abundance. He, however, also detected diel variations in relative abundance of amphipods and fish larvae which were not found in the present study. Diel variation and vertical migration in the sea remains a poorly understood subject and the differences seen in the present study remain to be satisfactorily explained.

SUMMARY

Evaluation of the biomass and composition of zooplankton in the Gulf of Mexico was undertaken. Plankton samples were collected during August and November by vessels of the National Marine Fisheries Service.

The zooplankton biomass in the Gulf of Mexico follows the same trends, with regard to magnitude and distribution, that have been found in other temperate and subtropical marine areas. Proximity to the coast and the effect of nutrient input of rivers appear to be the most important factors determining the amount of zooplankton present in this area. Biomass was greatest in continental shelf waters, intermediate in continental slope waters, and least in oceanic waters. Low salinity surface waters reflected the input of fresh water into the Gulf, especially from the Mississippi River, and zooplankton abundance was greater in these areas. Temperature and salinity normally had a greater range within the 200 m water column sampled at any station than was present for the surface waters of the study area. For this reason, zooplankton biomass variation could not be studied in terms of the hydrographic data. Zooplankton biomass of slope and oceanic waters in the upper 200 m was greater at night. The night increase resulted from diel migrations into this zone by some organisms at night from greater depths.

The most abundant animals present in the samples were copepods which comprised over 50 percent of the total. Based on overall means, only ostracods and chaetognaths of the remaining groups comprised more than 10 percent of the plankton. The relative composition of the zooplankton remained the same in shelf, slope and oceanic waters at the level of the taxonomic categories examined. Upward diel variation in slope and oceanic waters was noted for copepods, chaetognaths, mollusks, and tunicates.

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PART II

ABUNDANCE AND DIVERSITY AMONG COPEPODS
IN THE GULF OF MEXICO

INTRODUCTION

A thorough knowledge of the zooplankton is essential to understanding the processes occurring in any body of water. Copepods, by virtue of their numbers and trophic diversity, are an important element of any zooplankton community.

Few studies have been carried out on the copepods of the Gulf of Mexico. Early work on the copepods from this region has been reviewed by Schmitt (1954) and by Fleminger (1956). Published accounts of copepods from the Gulf of Mexico after that time are not numerous and are primarily taxonomic works, or deal with only a limited geographical area. Several studies deal with the entire zooplankton community of limited geographic areas adjacent to the coast and mention copepods only as a small part of the entire study. Grice (1960a, b) discussed 38 species of calanoid and cyclopoid copepods collected over a one year sampling period and provided figures and an identification key to members of the genus Oithona from the west coast of Florida. Dragovich (1961) included copepods, as a group, in a study on the plankton of the Naples, Florida region. Cuzon du Rest (1963) identified 11 copepod species from estuarine waters of Louisiana and noted the occurrence of several others which were not identified to species. Kelly and Dragovich (1967) considered copepods briefly in their study of the zooplankton of Tampa Bay, Florida. Thirty-five copepod species were identified by Hopkins (1966) from St. Andrews Bay, Florida and their abundance on a

seasonal basis was noted as part of a more extensive study of the zooplankton of this area. Acosta (1971) reported on the occurrence of 14 species from waters off the coast of Mississippi in an unpublished dissertation. Gillispie (1971) noted the occurrence of 34 species of copepod collected in coastal waters of Louisiana and presented data on the seasonal abundance of some species. Perry and Christmas (1973) identified and reported the seasonal occurrence of 31 copepod species collected in Mississippi Sound and Biloxi Bay, Mississippi. Bowman (1975) described Oithona colcarva and discussed its occurrence in coastal waters of the Gulf of Mexico.

Until recently, accounts of copepods from oceanic waters of the Gulf of Mexico were rare. Fleminger's (1956) dissertation reported on the occurrence, distribution and relative abundance of 97 species of calanoid copepods. He also provided identification keys for several genera and included ecological notes. This work resulted in several published taxonomic accounts (Fleminger, 1957a, b, c) including descriptions of new species, but much remains unpublished. Grice (1969) reported two new species and 20 new records of calanoid copepods from the Gulf of Mexico and Caribbean Sea. Park (1970) described 28 new species and noted 58 new records of calanoid copepods from this area. He also listed 178 calanoid species identified in his study and provided an identification key to the genus Spinocalanus. Bright *et al.* (1972) reported on the effect of a solar eclipse on the vertical distribution of several calanoid species in the Gulf of Mexico. Ferrari (1973, 1975) has reported on the occurrence and distribution of cyclopoid copepods of the families Oncaeidæ

and Corycaeidae from the Gulf of Mexico together with figures and an identification key to the genus Oncaea. The systematics of several calanoid genera has been treated in a series of publications by Park (1974, 1975a-d).

This study reports on the total number of copepods present in samples from the Gulf of Mexico and indicates their distributional pattern. Numbers of individuals of each species present in some of the samples have been determined and aspects of the diversity of the copepod fauna are discussed.

MATERIALS AND METHODS

The copepods from 180 zooplankton samples from the Gulf of Mexico and adjacent waters of the Caribbean Sea were examined. The samples were collected during August and November 1971 by the National Marine Fisheries Service (NMFS) and State University System Institute of Oceanography (SUSIO) of Florida. All samples were collected by means of oblique tows from the surface down to 200 m depth (depth permitting). A 60 cm Bongo-type sampler was used, which was equipped with a 0.333 mm mesh net on the side from which these samples were collected. A Tsurumi Precision Instrument Company (TSK) flowmeter measured the amount of water filtered by the sampler. Further details of sampling procedures, the location of stations and time of day of collection have been presented in part one of this paper.

The total number of calanoid and non-calanoid copepods in the aliquots used for determination of group composition was determined and the number of individuals of each computed for 100 cubic meters. All mature copepods were identified from aliquots of 96 samples which were collected in August, 1971. These included all samples on cruise 7129 of the R/V OREGON II and 11 samples collected at the same time by the R/V TURSIOPS. The samples were first examined under a binocular dissecting microscope and all species easily identifiable were noted. The remainder were removed for closer examination at a later date. They were subsequently stained with Acid Fuchsine and examined in

glycerine or a mixture of glycerine and lactic acid. The most useful works for identification were those of Wilson (1932), Rose (1933) and Owre and Foyo (1967). Numerous other publications dealing with specific genera or families were consulted to effect or verify identifications.

Statistical analyses were carried out with the Statistical Analysis System (Service, 1972) to detect differences among areas and time of collection for all species. Community indices were calculated for all samples in which the copepods had been identified. The Simpson Index (Simpson, 1949) and Shannon-Weiner Index (Shannon and Weaver, 1949) were selected as measures of species diversity. The richness component of diversity was considered to be the number of species present in a sample and four measures of species evenness were calculated following the method of Fager (1972).

The following terminology with regard to statistics applies throughout this paper. All species have been subjected to statistical analysis on an individual basis for abundance by area and by time of collection. The word "significant" or "statistically significant" means that differences were detected at the 0.05 percent level of probability. These terms are used in no other context. The phrase "highly significant" means that statistically significant differences were detected at the 0.01 percent level of probability. Similarly, "highly significant" is used in no other context in this paper.

RESULTS AND DISCUSSION

Limitations of the Data

Evaluation of data derived from zooplankton studies is subject to several limitations and no sampling program can overcome them all.

The sampling program and equipment used to collect samples exerts some bias on the results. The size of the mesh aperture used determines the minimum size of the organisms which will be retained in the net. The characteristics of retention of organisms in nets was discussed by Vannucci (1968). Several copepod species may not have been accurately sampled because their small size allowed some specimens to pass through the net.

Estimation of the abundance of planktonic organisms assumes that they are evenly dispersed within the immediate sampling area, a situation which is rare in nature. The patchy distribution of zooplankton in the ocean is well established. The reports of Longhurst *et al.* (1966) and Wiebe (1970) among others, demonstrate that differences in abundance occur within distances as small as a few meters. The relatively large volumes of water filtered for my study minimizes, but does not eliminate, this difficulty. Also associated with the spatial distribution of zooplankton is the problem of vertical stratification of organisms within the water column. Numerous zooplankters, including copepods, occupy a relatively narrow vertical range or are much more abundant in a certain depth interval. Animals occupying only a portion of the upper 200 m, or having a

variable abundance within it, will not be sampled accurately. There is much evidence to support the existence of vertical stratification of organisms and it now seems most extensive in the upper several hundred meters of the ocean. Barraclough *et al.* (1969) have demonstrated that an extensive population of Calanus cristatus exists between 35 and 40 m in waters of the north Pacific and outside of this depth interval numbers decrease rapidly. Roe (1972) has shown stratification of copepods in the upper 200 m of the eastern Atlantic. Owre and Foyo (1967) compiled considerable data on copepods showing variability in abundance at various depths in the Florida Current.

Seasonal differences in abundance are common for both coastal and oceanic waters (Parsons and Takahashi, 1973) and have been found for copepods in the Gulf of Mexico by Fleminger (1956). The samples used for my study were collected during a small part of the year, and, therefore, only represent what existed at that time. Other conditions may be expected at different times of the year, and variations from one year to another may also occur. Movement of animals into and out of the depth range sampled over the course of a day is another time-related source of variation affecting the results of zooplankton studies.

Because no study can compensate for all variables, it is especially important to be aware of their existence as conclusions are drawn and comparisons made.

Abundance of Copepods

The mean abundance of copepods for all samples was 5161 individuals/100 m³, representing 4692 calanoids/100 m³ and 469 non-calanoids/100 m³. Calanoids ranged from a minimum of 194/100 m³ to a maximum of 87993/100 m³. The range for non-calanoids was from zero to 5774/100 m³.

Calanoids were most abundant in waters over the continental shelf where a mean abundance of 10809/100 m³ was found; they were less abundant over the continental slope where the mean was 2175/100 m³; and least abundant in oceanic waters where the mean was 1680/100 m³. The difference in abundance among localities was significant for calanoids; however, no significant difference could be detected for the same three localities for non-calanoid copepods. There was no significant diel variation in abundance for either calanoid or non-calanoid copepods for stations where water depth exceeded 200 m, nor was any difference detected in waters over the continental shelf. The mean abundance of calanoid and non-calanoid copepods for the three localities for day and night collected samples is summarized in Table 7. The abundance of calanoid copepods at each station is shown on Figures 7-9 and for non-calanoid copepods on Figures 10-12.

One hundred and one species of planktonic copepods were identified from the samples. These represented three orders and 26 families. No new species were among those identified nor were any of the species previously unrecorded from the Gulf of Mexico. The overall mean abundance and the mean abundance for each locality by day and night for each copepod species found are shown in Table 8.

Table 7. Mean abundance (individuals/100 m³) for calanoid and non-calanoid copepods, with day and night means for all samples collected in water exceeding 200 m in depth.

	Calanoids	Non-calanoids
Continental Shelf	10809	614
Continental Slope	2175	507
Oceanic Waters	1680	343
Daylight Samples	2170	374
Night Samples	1902	390

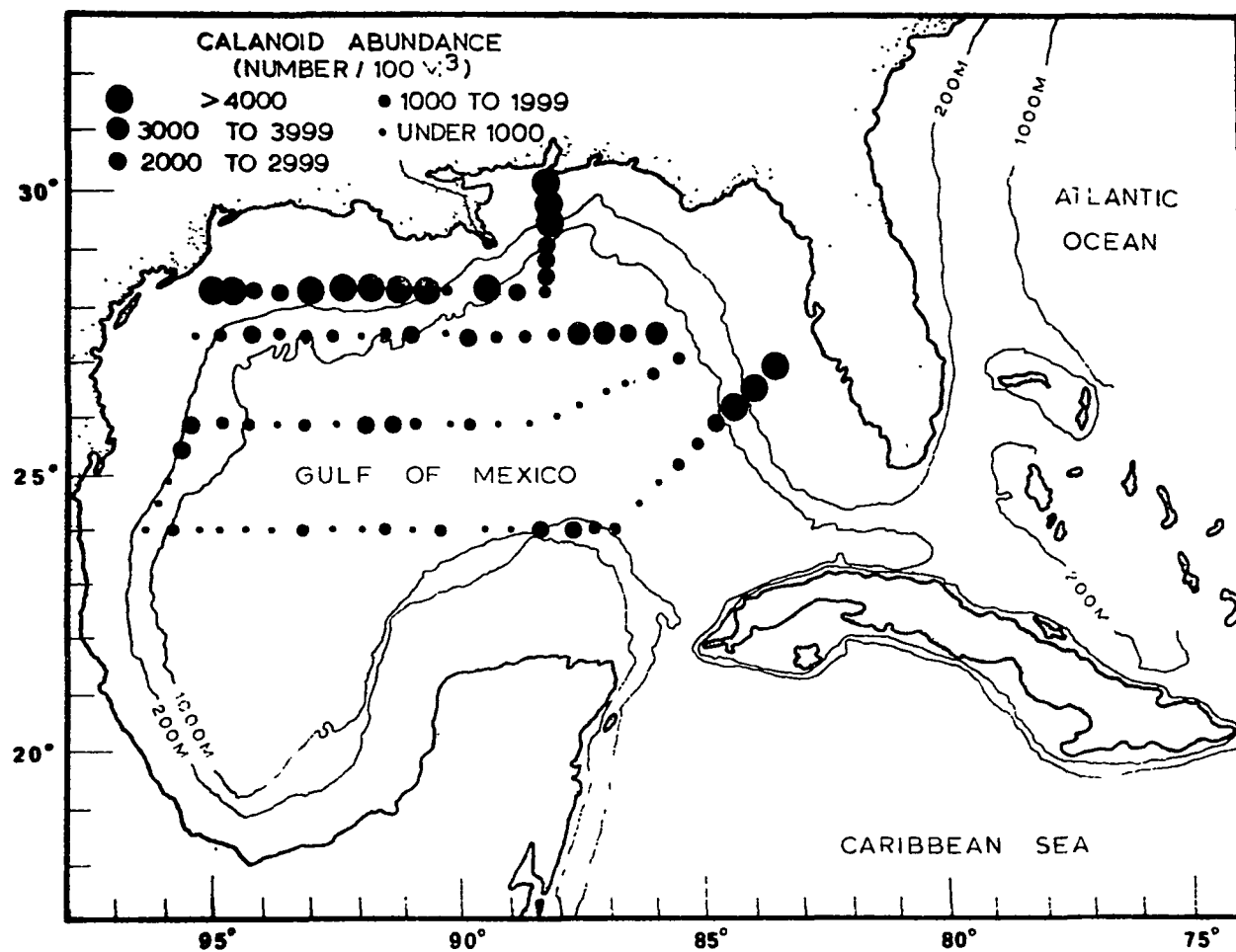


Figure 7. Abundance of calanoid copepods in August 1971 on R/V OREGON II cruise 7129.

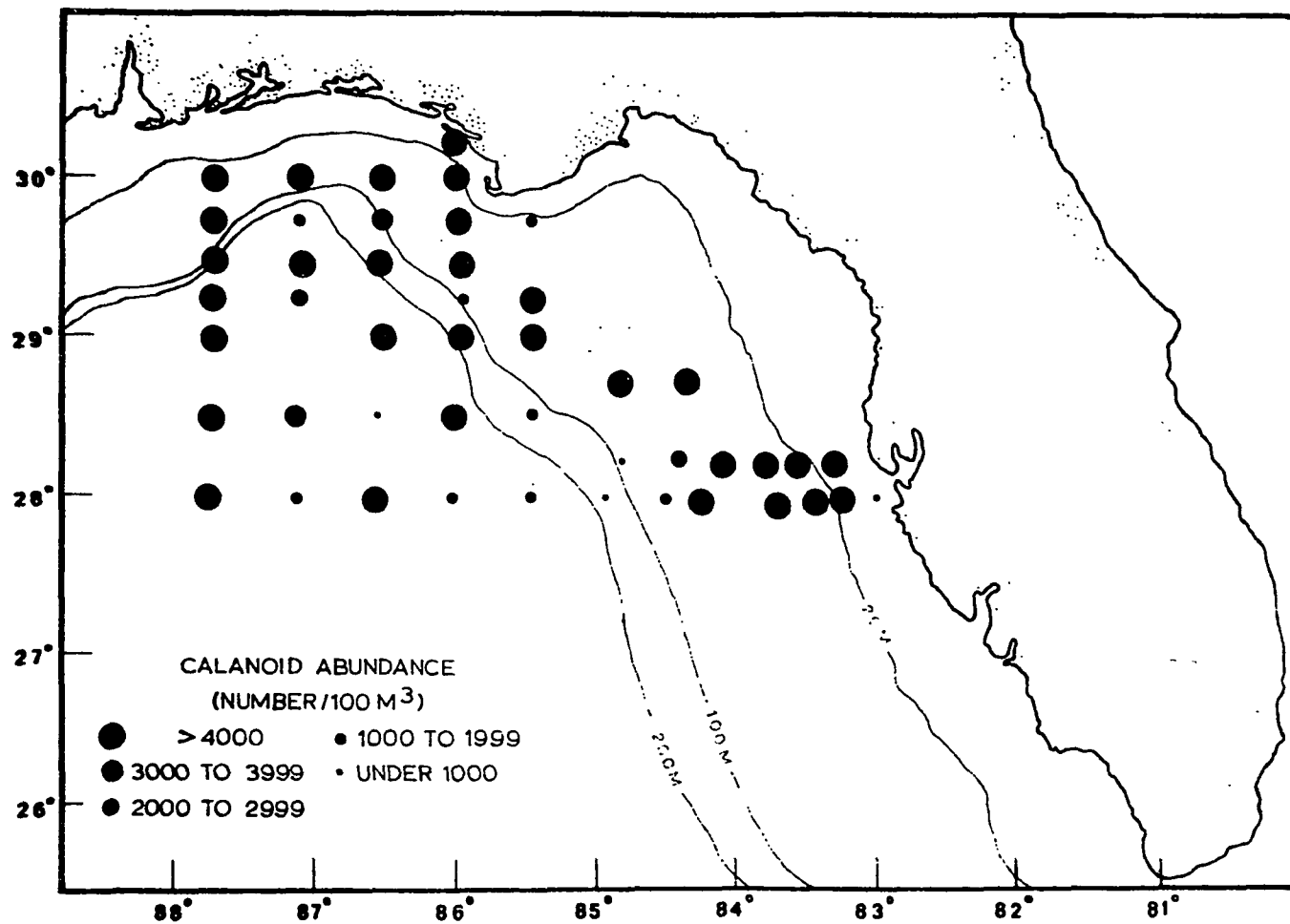


Figure 8. Abundance of calanoid copepods in August 1971 on R/V TURSIGPS cruise 7121.

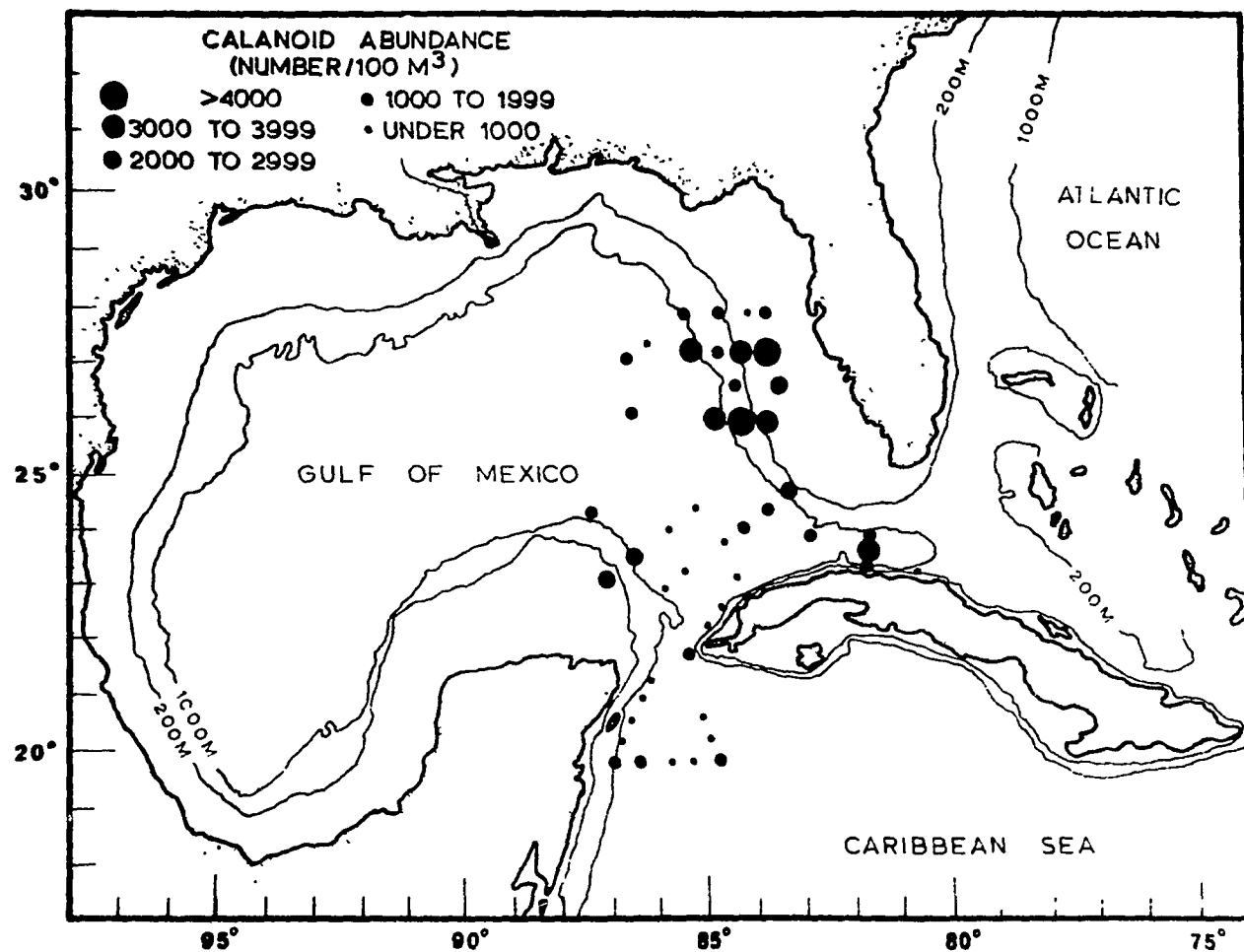


Figure 9. Abundance of calanoid copepods in November 1971 on R/V GREGON II cruise 7131.

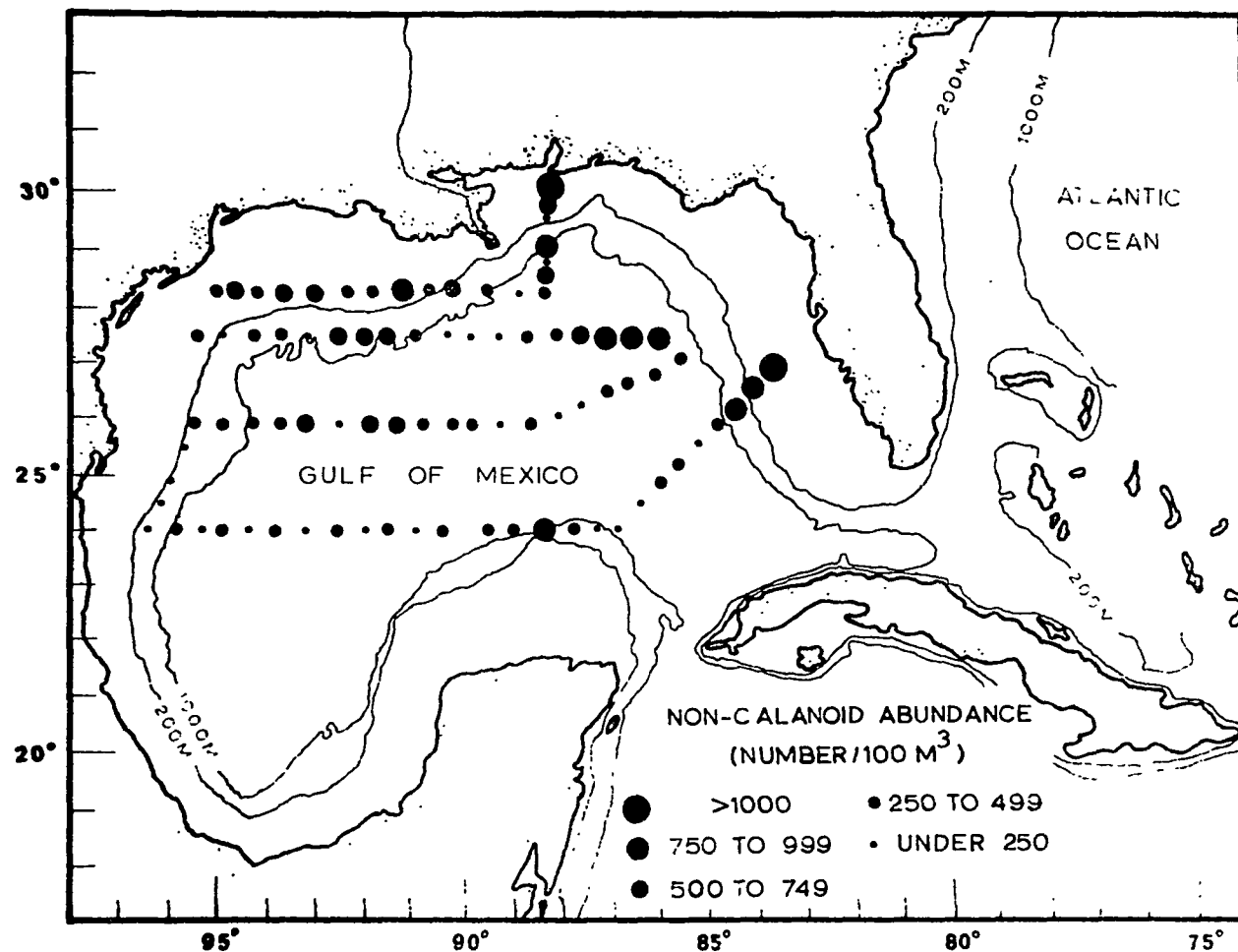


Figure 10. Abundance of non-calanoid copepods during August 1971 on R/V OREGON II cruise 7123.

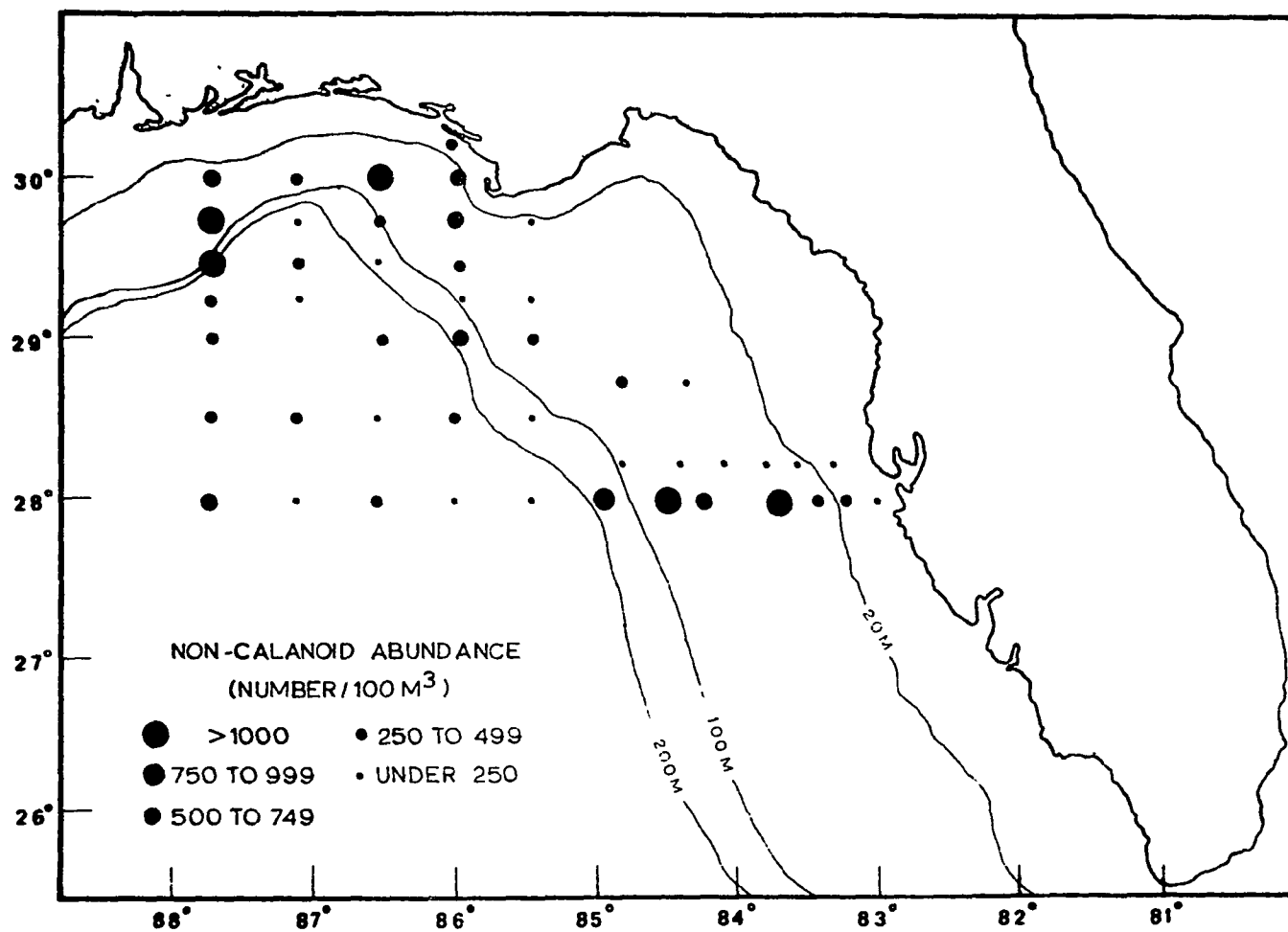


Figure 11. Abundance of non-calanoid copepods in August 1971 on V/V TURSIOPS cruise 7121.

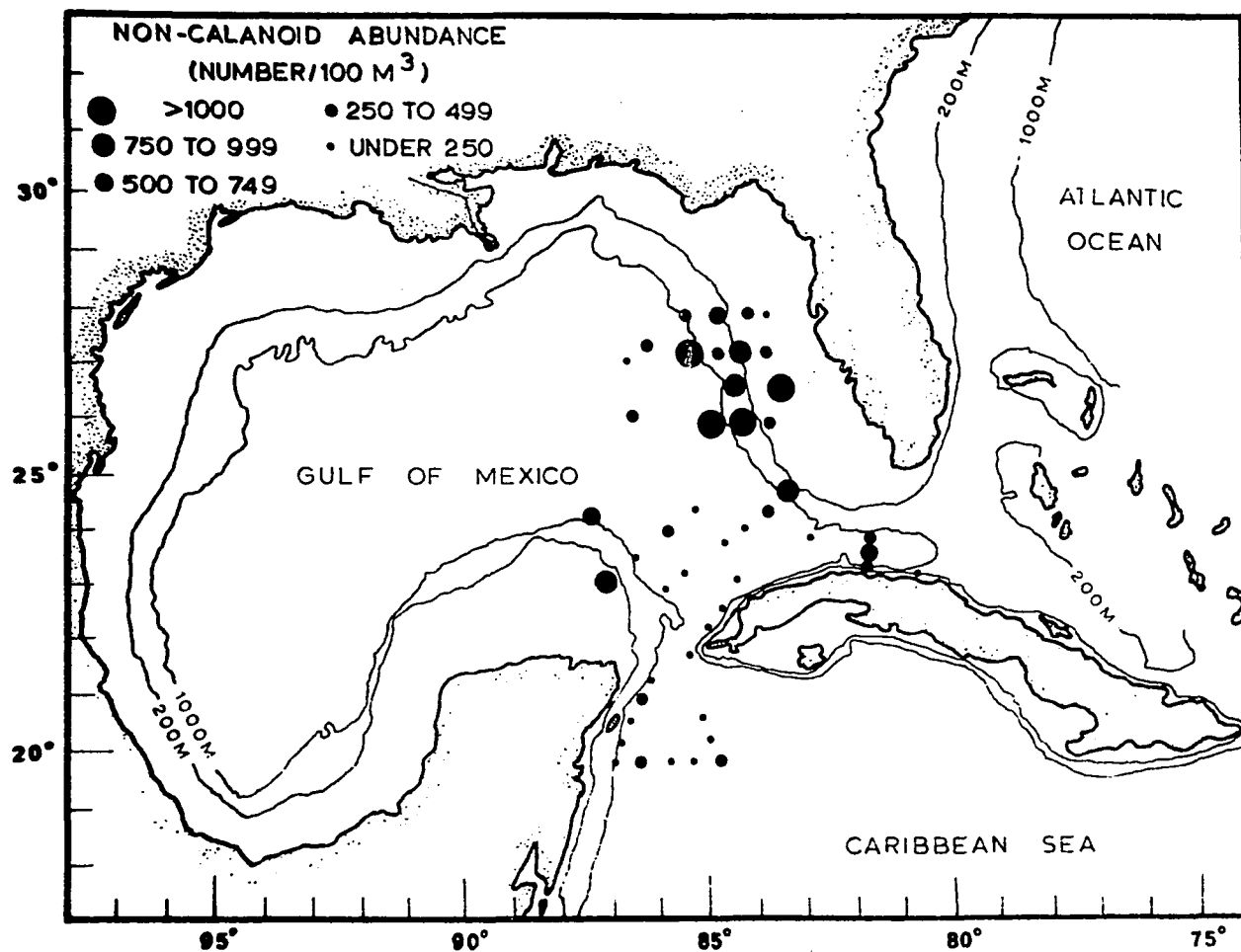


Figure 12. Abundance of non-calanoid copepods in November 1971 on R/V OREGON II cruise 7131.

Table 8. List of copepod species identified from all samples examined together with their mean abundance (individuals/100 m³) for the entire study, and each area for samples collected during daylight hours and at night. A + means that a species was present with an abundance less than one individual/100 m³, and an asterisk (*) means that a species was identified from a sample other than those analyzed in detail.

Species	All Samples	Day			Night		
		<u>Shelf</u>	<u>Slope</u>	<u>Oceanic</u>	<u>Shelf</u>	<u>Slope</u>	<u>Oceanic</u>
ORDER CALANOIDA							
Calanidae							
1. <u>Calanus tenuicornis</u> Dana, 1849	7	2	6	10	0	5	10
2. <u>Nannocalanus minor</u> (Claus, 1863)	128	91	182	147	121	79	134
3. <u>Neocalanus gracilis</u> (Dana, 1849)	3	6	5	3	0	3	3
4. <u>N. robustior</u> (Giesbrecht, 1888)	2	0	5	2	3	1	1
5. <u>Undinula vulgaris</u> (Dana, 1849)	403	922	210	274	986	263	220
Eucalanidae							
6. <u>Eucalanus crassus</u> Giesbrecht, 1888	3	0	0	7	0	3	+
7. <u>E. elongatus</u> Claus, 1866	+	6	0	0	0	0	0
8. <u>E. monachus</u> Giesbrecht, 1888	2	0	0	4	0	1	+
9. <u>E. pileatus</u> Giesbrecht, 1888	251	939	48	24	1050	102	41
10. <u>E. sewelli</u> Fleminger, 1974	14	16	17	16	8	11	14
11. <u>Mecynocera clausii</u> Thompson, 1888	+	0	1	+	0	+	+
12. <u>Rhincalanus cornutus</u> Schmaus, 1917	28	35	35	43	0	14	18

Table 8 continued.

Species	All Samples	Day			Night		
		<u>Shelf</u>	<u>Slope</u>	<u>Oceanic</u>	<u>Shelf</u>	<u>Slope</u>	<u>Oceanic</u>
Paracalanidae							
13. <u>Calocalanus pavo</u> Dana, 1849	21	56	26	23	7	15	7
14. <u>C. pavoninus</u> Farran, 1936	2	+	4	3	0	3	+
15. <u>Paracalanus aculeatus</u> Giesbrecht, 1888	18	50	28	5	51	6	9
Pseudocalanidae							
16. <u>Clausicalanus arcuicornis</u> (Dana, 1849)	1	0	0	3	0	0	1
17. <u>C. furcatus</u> (Brady, 1883)	17	10	5	8	113	4	5
18. <u>C. jobei</u> Frost and Fleminger, 1968	387	694	147	180	2025	87	113
19. <u>C. pergens</u> Farran, 1926	+	0	2	+	0	+	0
Aetideidae							
20. <u>Chirundina streetsi</u> Giesbrecht, 1895	+	0	0	0	0	2	+
21. <u>Euaetideus giesbrechti</u> (Cleve, 1904)	32	5	36	50	0	28	35
22. <u>Euchirella amoena</u> Giesbrecht, 1888	+	0	0	0	0	0	+
23. <u>E. messinensis</u> (Claus, 1863)	+	0	0	0	0	+	2
24. <u>E. pulchra</u> (Lubbock, 1856)	*						
25. <u>E. splendens</u> Vervoort, 1963	*						
26. <u>E. venusta</u> Giesbrecht, 1888	+	0	1	0	0	+	1
27. <u>Gaetanus miles</u> Giesbrecht, 1888	+	0	0	+	0	0	+
28. <u>G. minor</u> Farran, 1905	+	0	0	0	0	3	+
29. <u>Undeuchaeta major</u> Giesbrecht, 1888	+	0	0	0	0	0	2
30. <u>U. plumulosa</u> (Lubbock, 1856)	1	0	0	+	0	3	3

Table 8 continued.

Species	All Samples	Day			Night		
		<u>Shelf</u>	<u>Slope</u>	<u>Oceanic</u>	<u>Shelf</u>	<u>Slope</u>	<u>Oceanic</u>
Euchaetidae							
31. <u>Euchaeta marina</u> (Prestandrea, 1833)	108	152	63	5	251	72	80
32. <u>E. media</u> Giesbrecht, 1888	3	0	1	2	0	6	8
33. <u>E. paraconcinna</u> Fleminger, 1957	+	2	0	+	0	+	+
34. <u>E. spinosa</u> Giesbrecht, 1892	+	0	0	0	0	+	0
Phaennidae							
35. <u>Phaenna spinifera</u> Claus, 1863	2	0	1	2	0	2	5
Scolecithricidae							
36. <u>Scolecithricella dentata</u> Giesbrecht, 1892	18	18	31	17	0	17	23
37. <u>Scolecithrix bradyi</u> Giesbrecht, 1888	+	2	0	+	0	+	0
38. <u>S. danae</u> (Lubbock, 1856)	20	12	38	23	9	11	23
39. <u>Scottocalanus corystes</u> Owre and Foyo, 1967	+	0	0	0	0	+	1
40. <u>S. persecans</u> (Giesbrecht, 1895)	+	0	0	0	0	+	0
41. <u>S. securifrons</u> (T. Scott, 1894)	*						
Temoridae							
42. <u>Temora stylifera</u> (Dana, 1849)	167	342	95	75	669	54	93
43. <u>T. turbinata</u> (Dana, 1849)	558	622	147	245	2613	814	132

Table 8 continued.

Species	All Samples	Day			Night		
		<u>Shelf</u>	<u>Slope</u>	<u>Oceanic</u>	<u>Shelf</u>	<u>Slope</u>	<u>Oceanic</u>
Metridiidae							
44. <u>Pleuromomma abdominalis</u> (Lubbock, 1856)	41	41	12	19	10	34	99
45. <u>P. gracilis</u> (Claus, 1863)	50	19	18	16	65	117	82
46. <u>P. xiphias</u> (Giesbrecht, 1889)	4	0	1	+	0	4	12
Centropagidae							
47. <u>Centropages velificatus</u> (DeOliveira, 1947)	1033	2336	6	40	7621	88	2
Lucicutiidae							
48. <u>Lucicutia flavicornis</u> (Claus, 1863)	89	102	96	102	43	52	100
49. <u>L. ovalis</u> (Giesbrecht, 1889)	18	15	30	21	0	7	23
Heterorhabdidae							
50. <u>Heterorhabdus papilliger</u> (Claus, 1863)	13	2	6	26	0	6	13
51. <u>Heterostylites longicornis</u> (Giesbrecht, 1892)	1	0	4	0	0	5	2
Augaptilidae							
52. <u>Centraugaptilis rattrayi</u> (T. Scott, 1893)	+	0	0	0	0	0	+
53. <u>Haloptilis longicornis</u> (Claus, 1863)	1	0	4	0	0	5	2
54. <u>H. ornatus</u> (Giesbrecht, 1892)	10	3	9	15	6	10	8
55. <u>H. spiniceps</u> (Giesbrecht, 1892)	1	0	0	2	0	3	2

Table 8 continued.

Species	All Samples	Day			Night		
		<u>Shelf</u>	<u>Slope</u>	<u>Oceanic</u>	<u>Shelf</u>	<u>Slope</u>	<u>Oceanic</u>
Arietellidae							
56. <u>Arietellus setosus</u> Giesbrecht, 1892	+	0	0	+	0	+	3
Candaciidae							
57. <u>Candacia bipinnata</u> (Giesbrecht, 1889)	+	0	1	+	0	0	0
58. <u>C. curta</u> (Dana, 1852)	12	30	5	5	29	9	8
59. <u>C. longimana</u> (Claus, 1863)	28	84	12	21	41	16	16
60. <u>C. pachydactyla</u> (Dana, 1849)	4	7	0	6	0	1	3
61. <u>C. paenelongimana</u> Fleminger and Bowman, 1956	1	0	7	0	0	0	2
62. <u>Paracandacia bispinosa</u> (Claus, 1863)	7	0	2	10	0	6	9
63. <u>P. simplex</u> (Giesbrecht, 1889)	+	0	0	+	0	0	2
Pontellidae							
64. <u>Labidocera acutifrons</u> (Dana, 1852)	+	0	0	+	6	0	0
65. <u>L. aestiva</u> Wheeler, 1901	11	86	0	+	3	0	0
66. <u>L. nerii</u> (Kryer, 1849)	+	0	0	0	0	1	+
67. <u>Pontella meadii</u> Wheeler, 1901	11	79	0	0	0	6	0
68. <u>P. mimocerami</u> Fleminger, 1957	3	0	0	+	34	0	0
69. <u>P. securifer</u> Brady, 1883	3	4	0	+	12	3	1
70. <u>Pontellina plumata</u> (Dana, 1849)	+	0	0	0	0	0	+
71. <u>Calanopia americana</u> Dahl, 1894	22	42	1	2	168	+	+

Table 8 continued.

Species	All Samples	Day			Night		
		<u>Shelf</u>	<u>Slope</u>	<u>Oceanic</u>	<u>Shelf</u>	<u>Slope</u>	<u>Oceanic</u>
Acartiidae							
72. <u>Acartia danae</u> Giesbrecht, 1889	21	53	31	15	26	11	11
73. <u>A. tonsa</u> Dana, 1849	2	16	0	0	0	0	+
ORDER HARPACTICOIDA							
Aegisthidae							
74. <u>Aegisthus mucronatus</u> Giesbrecht, 1891	+	0	0	+	0	0	+
Clymenestridae							
75. <u>Clymenestra scutellata</u> Dana, 1848	1	9	9	+	0	7	+
Miraciidae							
76. <u>Miracia efferata</u> Dana, 1852	2	0	1	2	9	2	3
77. <u>Oculosetella gracilis</u> (Dana, 1852)	+	1	0	+	0	+	0
ORDER CYCLOPOIDA							
Oithonidae							
78. <u>Oithona plumifera</u> W. Baird, 1843	105	80	134	130	31	103	105

Table 8 continued.

Species	All Samples	Day			Night		
		Shelf	Slope	Oceanic	Shelf	Slope	Oceanic
79. <u>O. robusta</u> Giesbrecht, 1892	17	2	20	28	0	11	19
80. <u>O. setigera</u> (Dana, 1852)	5	0	23	7	0	3	2
Clausidiidae							
81. <u>Saphirella tropica</u> Wolfenden, 1906	+	0	0	+	0	+	+
Oncaeidae							
82. <u>Lubbockia squillimana</u> Claus, 1863	+	0	1	1	0	0	1
83. <u>Oncaea conifera</u> Giesbrecht, 1891	17	28	56	6	42	4	12
84. <u>O. mediterranea</u> Claus, 1863	183	165	349	216	330	114	119
85. <u>Pachos punctata</u> (Claus, 1863)	+	0	2	0	0	0	+
Sapphirinidae							
86. <u>Copilia mirabilis</u> Dana, 1852	9	26	15	4	15	10	3
87. <u>C. quadrata</u> Dana, 1852	1	0	9	1	0	3	1
88. <u>C. vitrea</u> (Haeckel, 1864)	+	0	0	+	0	0	0
89. <u>Sapphirina angusta</u> Dana, 1852	+	0	4	1	0	0	0
90. <u>S. metallina</u> Dana, 1852	9	4	12	9	0	12	12
91. <u>S. nigromaculata</u> Claus, 1863	18	24	11	11	49	26	11
92. <u>S. opalina</u> Dana, 1852	2	0	2	3	2	4	+
93. <u>S. ovatolanceolata</u> Dana, 1852	+	0	4	0	4	0	+

Table 8 continued.

Species	All Samples	Day			Night		
		<u>Shelf</u>	<u>Slope</u>	<u>Oceanic</u>	<u>Shelf</u>	<u>Slope</u>	<u>Oceanic</u>
Corycaeidae							
94. <u>Corycaeus clausi</u> F. Dahl, 1894	10	36	2	1	37	5	3
95. <u>C. flaccus</u> Giesbrecht, 1891	75	40	97	114	30	31	73
96. <u>C. latus</u> Dana, 1852	26	66	16	25	67	6	10
97. <u>C. lautus</u> Dana, 1852	10	1	7	9	0	14	17
98. <u>C. limbatus</u> G. Brady, 1883	30	11	33	45	0	18	34
99. <u>C. speciosus</u> Dana, 1852	63	10	49	42	163	48	40
100. <u>C. typicus</u> (Kryer, 1849)	17	6	17	23	25	23	7
101. <u>Farranula gracilis</u> (Dana, 1853)	19	73	12	13	5	6	13

The distribution of total copepod abundance followed closely the distribution of total biomass. The abundance of non-calanoïd copepods (almost exclusively cyclopoids) was more variable than that of calanoids. There was no significant difference among shelf, slope and oceanic waters for non-calanoïds. The taxonomic composition was different among areas, however. In continental shelf waters the cyclopoids are primarily members of the genera Oncaea, Corycaeus and Farranula, whereas, in slope and oceanic waters they are primarily members of the genera Oithona and different species of Corycaeus.

Few studies are available which provide quantitative data on the abundance of copepods in oceanic waters, although numerous reports exist for coastal areas. Furthermore, when quantitative data is presented, it is often in the form of relative abundance rather than absolute abundance in a specified volume of water.

The total number of calanoids found in the present study was similar to that reported by Grice (1961) for waters of the upper 500 m of the central equatorial Pacific. He found from about 360 to 5640 calanoids/100 m³ in samples collected with nets having mesh sizes of 0.369 to 0.65 mm. Grice and Hulsemann (1965) reported the following abundance of calanoids from various depths in waters of the north Atlantic: in the depth interval surface to 50 m from about 600 to 2200 calanoids/100 m³ at various stations; for the interval 50 to 100 m, the range was from 200 to 1700 calanoids/100 m³; and in the depth interval 100 to 200 m, the calanoid abundance ranged from about 100 to 750 individuals/100 m³. Park (1970) found from six to 35

calanoids/100 m³ for bathypelagic waters of the Gulf of Mexico. Grice and Hulsemann's (1965) values are for oceanic waters and are quite similar to values obtained in the present study for oceanic waters of the Gulf of Mexico. Deevey (1971) found from about 11,000 to 25,000 copepods/100 m³ in the upper 500 m of the waters of the Sargasso Sea, representing an annual mean of 15,070 copepods/100 m³. Deevey (1971) separated this figure into a mean of 8980 calanoids/100 m³ and a mean of 6090 non-calanoids/100 m³. The abundances she found were nearly twice the overall calanoid abundance determined in the present study and about four times as great as the value obtained for the oceanic waters of the Gulf of Mexico. The mean value for the abundance of non-calanoid copepods reported by Deevey (1971) was 12 times greater than the mean abundance for non-calanoids found in the present study. A portion of these discrepancies, especially for the generally smaller non-calanoids, undoubtedly resulted from the use of a smaller meshed (0.202 mm) net used by Deevey (1971).

The exact number of species of copepods which occur in the Gulf of Mexico is difficult to estimate. Park (1970) lists 178 calanoid species which he found in samples from the Gulf of Mexico and Caribbean Sea from extensive sampling to great depths. Fleminger (1956) found 97 species of calanoid copepods in collections made in surface waters of the Gulf, some of which were not found by Park (1970). These values compare with the total of 101 species in the present study. Additional records since that time add only a few species to the fauna. Based on available literature between 200 and 225 species of calanoids probably occur in the Gulf of Mexico.

Critical study of some genera may result in the description of new species and new records may be expected, but probably will not raise this number much.

Non-calanoid copepods have been studied less than calanoids. Ferrari (1973) lists 31 species belonging to the families Oncaeidae and Corycaeidae. An examination of the somewhat scattered literature suggests that the cyclopoid and harpacticoids total about 75-80 species in the Gulf of Mexico. My study, and others, indicate about 300 copepod species occur in the Gulf of Mexico.

The present study included about one-third of the total number of species of copepods expected to inhabit the Gulf of Mexico. Calanoid copepods numbered 76 species in the present study, 43 percent of the number reported by Park (1970) and 78 percent of the total number of calanoid species found by Fleminger (1956). Some species were found which did not appear on one or the other of the above-mentioned lists, but all species found have been previously reported from the Gulf of Mexico. Comparable numbers of species have been found in similar studies carried out in the Atlantic. Roe (1972) identified 212 species of calanoids from the eastern Atlantic near the Canary Islands. Bowman (1973) found about 100 species from samples collected off the coast of the southeastern United States. The former contained samples collected from considerable depths and the latter sampled the water column to a depth of only about 70 m. Owre and Foyo (1967) recorded 216 species of calanoid, harpacticoid, and cyclopoid copepods from the Florida Current region.

Systematic Account

Family Calanidae. The calanid fauna found was the same as that found by others in the Gulf of Mexico and adjacent regions of the Atlantic Ocean (Fleminger, 1956; Park, 1970; Bowman, 1973). Undinula vulgaris is well known as an abundant component of temperate and subtropical zooplankton in the Atlantic. Fleminger (1956) reported it to be one of the most common copepods in the Gulf of Mexico, where he also noticed its tendency towards greater numbers in neritic waters. Bowman (1973) reports this species present off the coast of the southeastern United States in approximately the numbers that this study found in the Gulf of Mexico. Nannocalanus minor was found in approximately the same numbers as in the study by Bowman (1973) who considers this species under the name Calanus minor. This species is described as oceanic by Fleminger (1956), who points out that his studies and others indicate it to be common in waters over the shelf as it was in the present study also. Neocalanus gracilis and N. robustior, both considered as members of the genus Calanus by Bowman (1973), appear to be limited to oceanic waters. Bowman (1973) and Fleminger (1956) suggest that these species migrate towards the surface at night, and Owre and Foyo (1967) provide evidence to support this. The latter also say that these two species are limited to the upper few hundred meters so the abundance indicated in the present study probably represents a reasonable estimate of the population. Calanus tenuicornis was found to be an oceanic species by both Bowman (1973) and Fleminger (1956). The present study supports this and the abundance seems similar to that reported by these authors.

Family Eucalanidae. Eucalanus pileatus was found in similar numbers to those reported by Bowman (1973) who found it to be a consistent member of the shelf assemblage which he described. Other members of the genus he reports as oceanic and present in much smaller numbers as was the case in the present study. Fleminger (1973) separated the species E. sewelli as a new species distinct from the population of E. attenuatus. Discussions of populations of E. attenuatus from the Atlantic and Gulf of Mexico are now referable to E. sewelli. It was the most abundant oceanic species of Eucalanus found in the present study. Rhincalanus cornutus follows the same general pattern of abundance and distribution that was found by Fleminger (1956) and Bowman (1973). Mecynocera clausi was considered strictly oceanic by Bowman (1973) which agrees with the situation found in the present study for this small copepod which may not have been fully retained by the net.

Family Paracalanidae. Calocalanus pavo and C. pavoninus are both generally regarded as strictly oceanic species by Bowman (1973). In the Gulf, Fleminger (1956) regarded C. pavo as primarily oceanic but not uncommon in neritic waters, but C. pavoninus was considered strictly an oceanic species. In the present study C. pavo was more abundant in slope and shelf waters than in oceanic waters but C. pavoninus was primarily oceanic in distribution. The difference in distribution was not statistically significant and may reflect only a few stations which had large numbers or presence in stations near the edge of the continental shelf. Both species are small copepods and the estimates made here are probably low due to escapement

through the meshes of the net. All specimens of Paracalanus found in the present samples were referable to P. aculeatus. Bowman (1973) shows this species to have an abundance similar to that reported for the Gulf in the present study. Taxonomic confusion over members of this genus has rendered some previous reports of Paracalanus species not wholly reliable. Paracalanus aculeatus may be more abundant in the Gulf than my study indicates because of failure of the net to retain all specimens.

Family Pseudocalanidae. The genus Clausocalanus was revised by Frost and Fleminger (1968) and much confusion seems to have existed in the enumeration of species in light of that work. There is, therefore, no basis for comparison between the present study and previous ones. Bowman (1973) and Roe (1972) failed to distinguish most members of the genus into the individual species and prior studies are not reliable. Clausocalanus furcatus, the only species easily identified, was present in numbers similar to those reported by Bowman (1973). Fleminger (1956) reported that this was the most abundant calanoid in some samples from the Gulf. It was never abundant in the present study, nor was it the most abundant species of this genus. Clausocalanus jobei was the most abundant copepod found representing this genus and on at least one occasion it was the most numerous copepod present in a sample. Since it was not described at the time Fleminger (1956) examined his samples, it is possible that it was confused with other species.

Family Aetideidae. Bowman (1973) found no members of this family to be common. The present study found Euaetideus giesbrechti

to be common in oceanic and slope waters but not limited to them. Fleminger (1956) cites its presence in the Gulf without comment. The observations of Bowman (1973) for the remaining species of this family recorded in his samples are also germane to the occurrence of the other species of aetideidae found in the present study. Most are limited to mesopelagic waters and their presence in the samples is the result of vertical migration at night into the epiplanktonic zone or chance capture of stray individuals. Examination of depth records for the various species in Owre and Foyo (1967) and Vervoort (1963) supports this.

Family Euchaetidae. Euchaeta marina was abundant in shelf waters in contrast to Bowman's (1973) observations. He considered it an indicator of oceanic water. It was present in my samples in numbers similar to those found by Bowman (1973). Euchaeta paraconcinna was found in small numbers in the present study whereas Park (1975c) reports it as common. Fleminger (1956) described the species but failed to comment on its abundance. Fleminger (1956) did state that this species inhabits the Florida Current, but it was not reported from that region by Bowman (1973) or Owre and Foyo (1967). Euchaeta media and E. spinosa both appear to be inhabitants of deeper water which were represented in the present study only by stray individuals.

Family Phaennidae. Phaenna spinifera was reported to occur off the coast of the southeastern United States by Bowman (1973) in essentially the same pattern that was found in the present study. Fleminger (1956) reports its presence in the Gulf without comment.

Family Scolecithricidae. Scolecithricella dentata was the only representative of this genus identified from the present samples. It was the most abundant member of this genus found by Bowman (1973) who reported an abundance which was comparable to that in the present study. Bowman (1973) and Fleminger (1956) both considered this to be an oceanic species, in agreement with the results of the present study. Scolecithrix bradyi was uncommon and strictly oceanic according to both Bowman (1973) and Fleminger (1956) as it also was in the present study. Scolecithrix danae was found in numbers comparable to those found by Bowman (1973). Both Bowman (1973) and Fleminger (1956) considered this to be an oceanic species. I found it in shelf waters also, but at lower abundances than in slope and oceanic waters. All three species of Scottocalanus were strictly from slope or oceanic waters as were records of this genus by Bowman (1973), Fleminger (1956) and Owre and Foyo (1967). This genus generally inhabits deeper water and the occurrences reported here are of stray individuals or individuals which have migrated into the upper 200 m during the night.

Family Temoridae. Both Temora stylifera and T. turbinata were found in numbers comparable to those reported by Bowman (1973). Both species were also reported present in moderate numbers throughout the Gulf by Fleminger (1956), but I regard T. turbinata as very abundant in the Gulf. Both of these authors (Fleminger, 1956; Bowman, 1973) noted that when one species was abundant the other was often absent, suggesting that they were in competition with one another. Bowman (1973) also noted a seasonal difference in abundance which could

indicate both a spatial and temporal partitioning of the environment. Like Bowman's (1973) observations, I observed that T. turbinata was more abundant near land than was T. stylifera, although both were more abundant in shelf waters than in oceanic waters.

Family Metridiidae. Members of the genus Pleuromomma are well established as oceanic species with great proclivity towards vertical migration (Owre and Foyo, 1967; Moore and O'Berry, 1957). In the present study all species were more abundant in slope and oceanic waters and at night, supporting those observations. The species found were present in numbers similar to those reported by Bowman (1973). Bowman (1973) found two closely related species, P. gracilis and P. piseki, present in samples from waters off the coast of the southeastern United States. The confusion that exists in the literature between these two species has been discussed by Owre and Foyo (1967). All specimens found in the present study were referable to P. gracilis. Pleuromomma piseki is not reported in the literature from the Gulf although it occurs in adjacent waters. A critical study of the genus as it occurs in the Gulf of Mexico would seem a worthwhile endeavor.

Family Centropagidae. Centropages velificatus has previously been discussed as C. furcatus in the literature for the Atlantic Ocean. The abundance of this species was comparable to that reported by Bowman (1973) who noted it as an indicator of shelf waters. The observations of Bowman (1973), Fleminger (1956) and the present study indicate that this is a copepod which is fairly well restricted to shelf waters.

Family Lucicutidae. The two species of Lucicutia found in the present study were both basically oceanic in distribution. This agrees with what Bowman (1973), Fleminger (1956), and Grice and Hart (1962) have reported. Lucicutia flavicornis was present in numbers similar to those found by Bowman (1973). Lucicutia gaussae was found by Bowman (1973) but was not identified in the present study. Lucicutia ovalis was found but was much less abundant than L. flavicornis. Fleminger (1956) has also recorded L. ovalis from the Gulf.

Family Heterorhabdidae. Both species of Heterorhabdus found were oceanic and occurred in small numbers. Similar results were reported by Bowman (1973) and Fleminger (1956) for this group of copepods. No quantitative data are available in the literature for comparisons of abundance.

Family Augaptilidae. A single specimen of Centraugaptilus rattrayi was collected at night in oceanic waters. This copepod was not reported by either Bowman (1973) or Fleminger (1956), but has been reported from depths exceeding 200 m in the Gulf by Park (1970). Other records, some from within the upper 200 m, are given in Owre and Foyo (1967). This copepod appears to be a mesopelagic or bathypelagic species which may migrate at night or stray into the upper 200 m. The three species of Haloptilis recorded were all essentially oceanic and have been reported previously from the Gulf by Fleminger (1956), Park (1970) or Owre and Foyo (1967). None was ever abundant, which agrees with the general descriptions given by Bowman (1973). Quantitative estimates of abundance from the area or comparable areas are not available in the literature for these species.

Family Arietellidae. Only a few specimens of Arietellus setosus were found and they probably represent stray individuals or individuals which were migrating during darkness into the upper 200 m. This species was represented by a single individual in the collections of Bowman (1973) and was absent from Fleminger's (1956) samples. Park (1970) has reported it from deep water samples in the Gulf.

Family Candaciidae. Members of this genus are regarded as oceanic by Bowman (1973). All of the species that I found in the Gulf were among those reported by Bowman (1973). The abundance of Candacia curta was similar to that reported by Bowman (1973). The abundance of C. bipinnata and C. pachydactyla appears similar also but the abundance is so low in both studies that comparisons based on Bowman's (1973) figures are not easily made. In contrast to Bowman's (1973) observations, C. curta was more abundant in shelf waters than in oceanic waters. A similar pattern of distribution for this species in the Gulf was noted by Fleminger (1956) who found it more abundant in outer shelf and slope waters. Candacia longimana I found to be more abundant in shelf waters than in the other areas in contrast to the previous studies of Bowman (1973) and Fleminger (1956). Paracandacia bispinosa and P. simplex had distributions similar to those reported by Bowman (1973) and Fleminger (1956). Bowman (1973) reported the two species present in about equal numbers but in my study, P. bispinosa was more abundant than P. simplex.

Family Pontellidae. Pontellid copepods are mainly surface dwelling forms and are therefore not representatively sampled by

oblique tows. The distribution of all species found follows almost exactly the pattern described by Bowman (1973) for these species in the waters off the coast of the southeastern United States. The abundance of the species is not strictly comparable due to the depth to which the oblique tow was made, but the numbers appear to be of the same magnitude as those found by Bowman (1973) and Fleminger (1956) for species of Labidocera and Pontella. Pontellina plumata was limited to oceanic waters where it had very low abundance which agrees with Bowman's (1973) results. Both the abundance and distribution of Calanopia americana were similar to that reported by Bowman (1973), for his cruises made in summer and fall months.

Family Acartiidae. Acartia danae was present in numbers similar to those reported by Bowman (1973) and had a similar distribution to that reported by Bowman (1973) and Fleminger (1956).

Acartia tonsa was taken only occasionally in the present study. This species was very abundant, often comprising nearly 100 percent of the copepods in Bowman's (1973) study. He considered this species to be strictly limited to inshore waters. Acartia tonsa occurs in large numbers in inshore waters of the Gulf and I have collected samples predominantly composed of A. tonsa from estuarine waters of Louisiana. The low abundance in the present study results from the paucity of stations sufficiently close to land for this species to be collected.

Family Aegisthidae. Only a few specimens of Aegisthus mucronatus were found in scattered oceanic stations which agrees with the few other reports of this species from the western Atlantic. Owre and Foyo (1967) cite previous records in the area for this species.

Family Clymenestridae. The few individuals of Clymenestra scutellata found preclude any definite statement on its distribution. It appears to be present in greater numbers in shelf and slope waters but has been found at depths of 750 m (Owre and Foyo, 1967). Other workers have found C. scutellata in oceanic waters as cited in Owre and Foyo (1967), who reported it as occurring in small numbers.

Family Miraciidae. Both Miracia efferata and Oculosetella gracilis were found in very small numbers, but also occurred in numerous samples. There was no clear pattern of distribution for either species. Miracia efferata is reported as both common and rare in citations reviewed by Owre and Foyo (1967). Oculosetella gracilis appears to be a rare species based on previous accounts cited by Owre and Foyo (1967) which report it from the Atlantic. The small size of these two species may have resulted in underestimates of their abundance due to escape through the meshes of the net.

Family Oithonidae. The abundance of the three species of Oithona found in the present study seems to be similar to that reported by others for the same species (Owre and Foyo, 1967), although actual numerical abundances are not available for comparison. Owre and Foyo (1967) report O. plumifera to be common and O. robusta and O. setigera to be fairly common, which applies to the present study also.

Family Clausidiidae. Only a few specimens of Saphirella tropica were found and they were from oceanic waters. The status of this genus is in a state of confusion. Owre and Foyo (1967)

have reviewed previous records and summarized the taxonomic status of the genus. Regardless of its taxonomic status, it appears to be a rare species in all studies.

Family Oncaeidae. Lubbockia squillimana is considered abundant by Owre and Foyo (1967) and common by Ferrari (1973), the latter reporting it present at up to 80 individuals/100 m³. In the present study, however, it was rare, occurring infrequently and in small numbers. This is a small copepod and may not be retained by the net. Oncaea conifera was considered common by Owre and Foyo (1967) and Ferrari (1973) reported it present in the Gulf of Mexico with abundances of up to 500 individuals/100 m³. I found this species to be much less abundant, never having an abundance more than about one-tenth that reported by Ferrari (1973). Oncaea mediterranea was considered relatively common by Owre and Foyo (1967) and common by Ferrari (1973). The abundance seen in the present study is very similar to that reported by Ferrari (1973) from the Gulf. Pachos punctata was found infrequently in the present study and was considered rare by Owre and Foyo (1967) and Ferrari (1973).

Family Sapphirinidae. Comparative quantitative data on abundance are not available for members of this family. The three species of Copillia found in the present study were found in the same order of abundance in records cited by Owre and Foyo (1967): Copillia mirabilis was most common followed by C. quadrata and C. vitrea, the last species being rare. The general qualitative comments presented by Owre and Foyo (1967) on species of Sapphirina appear to apply to the species identified in the present study also. No species was ever abundant.

Family Corycaeidae. The corycaeid fauna identified was similar to that found in the Gulf by Ferrari (1973) and in the Florida Current region by Owre and Foyo (1967). The most abundant species in both of those studies and in the present study were Corycaeus flaccus and C. speciosus. All species found in the present study had mean estimated abundances from a third to a tenth as great as those found by Ferrari (1973). About a third of the samples used by Ferrari (1973) were collected with a net having a mesh size of 0.216 mm, the remainder were collected with a net having the same mesh size used in the present study. Mesh differences probably account for a portion of this difference in abundance.

Geographic Variation

Significant differences in abundance among continental shelf, continental slope, and oceanic waters were detected for 31 copepod species (Table 9). These formed two groups of species. One group of 16 may be regarded as shelf species, and the remaining group of 15 may be regarded as primarily oceanic species. These results generally agree with those of Bowman (1973) for waters off the coast of the southeastern United States in the Atlantic Ocean and the observations of Fleminger (1956) in the Gulf of Mexico for the same species.

Slope waters often had abundances intermediate to shelf and oceanic waters for both groups; however, this area was more like the oceanic in terms of its copepod fauna. Three species, Haloptilis longicornis, Candacia paenelongimana, and Oithona setigera had

Table 9. Mean abundance (individuals/100 m³) in each area of those copepod species having statistically significant differences among areas. Group A was more abundant in shelf waters; Group B was more abundant in slope or oceanic waters.

Species	Continental Shelf	Continental Slope	Oceanic
Group A			
<u>Undinula vulgaris</u>	954	236	247
<u>Eucalanus pileatus</u>	994	75	33
<u>Clausocalanus furcatus</u>	62	4	6
<u>C. jobei</u>	1360	117	147
<u>Euchaeta marina</u>	202	68	87
<u>Temora stylifera</u>	506	75	84
<u>T. turbinata</u>	1617	481	189
<u>Centropages velificatus</u>	4979	48	21
<u>Candacia curta</u>	29	7	6
<u>C. longimana</u>	62	14	19
<u>Pontella securifer</u>	8	2	1
<u>Calanopia americana</u>	105	1	1
<u>Sapphirina nigromaculata</u>	37	19	11
<u>Corycaeus clausi</u>	37	2	2
<u>C. latus</u>	62	11	18
<u>C. speciosus</u>	137	49	41
Group B			
<u>Calanus tenuicornis</u>	1	6	10
<u>Gaetanus minor</u>	0	1	<1
<u>Pleuromomma abdominalis</u>	25	23	69
<u>P. xiphias</u>	0	3	6
<u>Lucicutia flavicornis</u>	73	74	101
<u>Haloptilis longicornis</u>	0	4	<1
<u>Candacia paenelongimana</u>	0	4	1
<u>Paracandacia bispinosa</u>	0	4	10
<u>Oithona plumifera</u>	55	119	117
<u>O. robusta</u>	1	15	23
<u>O. setigera</u>	0	13	4
<u>Pachos punctata</u>	0	1	1
<u>Sapphirina metallina</u>	2	12	10
<u>Miracia efferata</u>	0	1	2
<u>Corycaeus limbatus</u>	6	25	40

abundances which suggest that they might be most successful in slope waters. They have been regarded as oceanic forms in other studies (Owre and Foyo, 1967; Bowman, 1973). Gaetanus minor was regarded as a slope species in the Gulf by Fleminger (1956) and the data in my study support this, but it was found too infrequently for the difference to be statistically significant.

Diel Variation

The 15 species for which significant diel variations in abundance occurred (Table 10) include species in which vertical migration is well known. Since the present study sampled the entire upper 200 m, only migration into or out of this portion of the water column has been measured. Any migrations which might occur within the upper 200 m will not have been detected.

Of the eight species significantly more abundant during daylight hours, one, Calocalanus pavo, is previously reported as undergoing a "reverse" vertical migration. Roehr and Moore (1965) report that C. pavo was present at greater depth during hours of darkness and was found in shallower water during daylight hours. Such a migration into the upper 200 m from greater depths during the day could explain the greater daytime abundance that was observed in the present study. The other two calanoids in this group are both oceanic species like C. pavo but have not been reported as migrating into surface waters during the day. Lucicutia flavicornis is reported to migrate upward at night by Owre and Foyo (1967); L. ovalis appears not to have been previously studied with regard to its diel pattern of abundance. The remaining five species that showed greater abundance during daylight

Table 10. Mean abundance (individuals/100 m³) of those copepod species having significantly different abundances between samples collected during daylight hours and at night. Group A was more abundant during daylight hours; Group B was more abundant at night.

Species	Day	Night
Group A		
<u>Calocalanus pavo</u>	35	10
<u>Lucicutia flavicornis</u>	100	64
<u>L. ovalis</u>	22	10
<u>Oithona setigera</u>	10	2
<u>Pachos punctata</u>	1	<1
<u>Sapphirina angusta</u>	1	0
<u>Corycaeus flaccus</u>	84	45
<u>Farranula gracilis</u>	33	8
Group B		
<u>Gaetanus minor</u>	0	1
<u>Undeuchaeta plumulosa</u>	<1	2
<u>Temora turbinata</u>	338	1187
<u>Pleuromomma gracilis</u>	18	88
<u>P. xiphias</u>	<1	5
<u>Clausocalanus furcatus</u>	8	11
<u>C. jobei</u>	340	742

hours were cyclopoid species having relatively low estimated abundances. The present data seem insufficient to serve as proof for any upward daylight migration of these species, although it serves to suggest this as a possible area for future study.

Of those species showing significantly greater abundance during hours of darkness, all but Temora turbinata and Clausocalanus jobei have been previously reported as being species with well established patterns of diel vertical migration towards the surface at night (cf. Owre and Foyo, 1967; Bowman, 1973; Roehr and Moore, 1965). The evidence supporting a migration by Clausocalanus furcatus is not extensive but is supported by the collections studied by Owre and Foyo (1967). The related C. jobei appears to have not been previously studied with regard to its diel distribution in the water column. The results of the present study strongly suggest that this species undergoes an upward migration at night, but additional investigation sampling at selected depths and times is needed for support. Temora turbinata is regarded as an epiplanktonic species associated with neritic waters (Fleminger, 1956; Bowman, 1973; Owre and Foyo, 1967). Owre and Foyo (1967) report this species as having a depth range of from the surface to 1750 m so it seems likely that a portion of the population residing below 200 m migrates upward at night and accounts for the greater abundance during night hours.

The Ten Most Abundant Species

Fourteen species were required to compile lists of the 10 most abundant copepods for each area and the overall study (Table 11). The most abundant species found in the present study are about the same

Table 11. The ten most abundant copepod species for the overall study, and each area together with the mean abundance of each species in each area (individuals/100 m³).

All Samples		Continental Shelf	
<u>Centropages velificatus</u>	1033	<u>Centropages velificatus</u>	4979
<u>Temora turbinata</u>	558	<u>Temora turbinata</u>	1617
<u>Undinula vulgaris</u>	403	<u>Clausocalanus jobei</u>	1359
<u>Clausocalanus jobei</u>	387	<u>Eucalanus pileatus</u>	994
<u>Eucalanus pileatus</u>	251	<u>Undinula vulgaris</u>	954
<u>Oncaea mediterranea</u>	183	<u>Temora stylifera</u>	506
<u>Temora stylifera</u>	167	<u>Euchaeta marina</u>	202
<u>Nannocalanus minor</u>	127	<u>Oncaea mediterranea</u>	192
<u>Euchaeta marina</u>	108	<u>Calanopia americana</u>	122
<u>Oithona plumifera</u>	105	<u>Nannocalanus minor</u>	106
Continental Slope		Oceanic Waters	
<u>Temora turbinata</u>	481	<u>Undinula vulgaris</u>	246
<u>Undinula vulgaris</u>	235	<u>Temora turbinata</u>	189
<u>Oncaea mediterranea</u>	231	<u>Oncaea mediterranea</u>	161
<u>Nannocalanus minor</u>	130	<u>Clausocalanus jobei</u>	147
<u>Oithona plumifera</u>	119	<u>Nannocalanus minor</u>	141
<u>Clausocalanus jobei</u>	117	<u>Oithona plumifera</u>	117
<u>Temora stylifera</u>	75	<u>Lucicutia flavicornis</u>	101
<u>Eucalanus pileatus</u>	75	<u>Corycaeus flaccus</u>	94
<u>Lucicutia flavicornis</u>	74	<u>Euchaeta marina</u>	87
<u>Euchaeta marina</u>	68	<u>Temora stylifera</u>	84
<u>Farranula gracilis</u>	68		

as those found in comparable studies by Grice and Hart (1962) and Bowman (1973) in the western Atlantic, and Fleminger (1956) in the Gulf of Mexico. Most studies unfortunately limit themselves to discussions of the calanoid fauna and there is little available information on non-calanoid species.

Bowman (1973) used 13 species, which he considered to be among the most abundant, to construct his affinity dendrograms. Eight of these species also appear on the lists of the 10 most abundant species which have been compiled for the present study. Several species (Acartia tonsa, Labidocera aestiva and Paracalanus spp.) were probably not common to both lists because the present study did not include samples collected from sufficiently close to land to include their areas of greatest abundance. Clausocalanus furcatus was very common in Bowman's (1973) study but C. jobei was not identified. The latter species was one of the most abundant species found in the present study. Since no extensive studies have taken place since the revision of this genus by Frost and Fleminger (1968), in which the species C. jobei was erected, comparisons within this genus cannot reliably be made. Roe (1972) has similarly avoided a consideration of members of this genus due to taxonomic difficulties. The present study and other studies which discuss the genus point out, however, that it contains several species which are important components of the copepod fauna.

Fleminger (1956) did not rank the species of calanoids which he identified from the Gulf in order of abundance. He did, however, establish six groupings of copepods that he considered characteristic

of different areas which can be discussed in context with present considerations. Three of his groups cannot appropriately be discussed. The estuarine species (groups 5 and 6) and the coastal species (group 4) are made up of species collected in areas not sampled by the present study well enough to be compared. Many of the species placed in those groups were not found in the present study or were present in only small numbers. With few exceptions the species common to both Fleminger's (1956) list and the present lists showed the same distributional pattern. Undinula vulgaris ranked fifth in abundance in shelf waters, third in abundance in slope and first in oceanic waters. It was, however, nearly four times more abundant in shelf waters than in the other areas. Fleminger (1956) considered this as a slope-oceanic species having neritic tendencies. Based on data from the present study, I would classify it as a shelf species with regard to numerical abundance but as a slope and oceanic species with regard to relative abundance. This species probably should not be considered an indicator of oceanic water and its success in all areas suggests that some factors such as availability of food, may be of more importance than physical characteristics of these three areas.

Fleminger (1956) also includes the congeners Temora stylifera and T. turbinata as slope-oceanic species, putting them into a sub-group separate from other slope-oceanic species. Based on the results of the present study, these species could both be classified as shelf species that are also successful in slope and oceanic waters. This is especially true for T. turbinata which is about three and

nine times more abundant in shelf waters than in slope or oceanic waters, respectively, although it is the most abundant species in slope waters. Temora stylifera is approximately six times more abundant in shelf waters than in either slope or oceanic waters where its abundance is about equal. Other authors (Owre and Foyo, 1967; Bowman, 1973) have noted the affinity of T. turbinata for proximity of land masses, and this situation prevails in the present study for the Gulf of Mexico also. Fleminger (1956) has commented briefly on the possibility of competition between these two species influencing their distribution and Bowman (1973) has pointed out that when one species is abundant the other is usually not. Owre and Foyo (1967) present data on the depths which these species inhabit which may indicate some vertical stratification separates the species. A more critical study of this congeneric association from the standpoint of resource allocation and utilization would seem to be a worthwhile endeavor. The remaining species listed by Fleminger (1956) seem to conform to what would be inferred from the lists compiled for the present study. It is clear from the discrepancies that exist, however, that the factors responsible for zonation in the upper 200 m of the sea remain to be fully explained.

Population Parameters

Population parameters calculated for the copepod species include measures of species diversity, richness and evenness (Table 12). Statistically significant or highly significant differences in the mean value of each parameter were detected among shelf, slope, and

Table 12. Mean values of several population parameters calculated for each area. Natural logarithms have been used in all calculations requiring log functions.

Index	Continental Shelf	Continental Slope	Oceanic Waters
<u>Species Diversity</u>			
Shannon-Weiner	2.059	2.691	2.823
Simpson's Index	0.754	0.870	0.912
<u>Species Richness</u>			
Number of Species	19	29	30
<u>Species Evenness</u>			
Scaled Simpson Index	0.799	0.901	0.933
Scaled Shannon-Weiner Index	0.719	0.870	0.934
Scaled Number of Moves Index	0.332	0.376	0.403
Scaled Standard Deviation Index	0.582	0.729	0.773

oceanic waters. No statistically significant differences were detected for any of these parameters when the samples were grouped by day or night time of collection.

Species Diversity. The usefulness and biological meaning of indices of diversity continue to be subjects of controversy. Discussions of various parameters proposed to measure diversity and its components, and considerations of their merits and shortcomings, may be found in review papers, including those by MacArthur (1965), Hurlbert (1971), Fager (1972), DeBenedictis (1973), and Goodman (1975).

The Simpson Index (Simpson, 1949) measuring the probability of interspecific encounters (cf. Hurlbert, 1971), and the Shannon-Weiner information theoretic index (Shannon and Weaver, 1949) were used to measure diversity. In this study, diversity was 1.3 times greater in slope waters than in continental shelf waters, when measured by the Shannon-Weiner Index, and 1.4 times greater in oceanic waters than in shelf waters. Slope waters were 1.15 times as diverse as shelf waters and oceanic waters were 1.20 times as diverse as shelf waters when measured by the Simpson Index.

Few studies have been made which lend themselves to comparison with the present. Generally, the magnitude of the values found in the present study are similar to those in the literature which have been calculated for other communities, especially marine benthic communities (Boesch, 1972; Watling, 1975) and for marine phytoplankton communities (Patten, 1962; Margalef, 1968). Application of diversity indices to zooplankton communities appears almost absent

from the literature. The values reported for the copepod portion of the zooplankton of Norwegian fjords reported by Stromgren (1975) are of the same magnitude as are those calculated in the present study for the same index.

Species Richness. The number of species present in each sample is often considered a measure of species richness. Several attempts have been made to establish and define the relationship between sample size and species richness (Sanders, 1968; Hurlbert, 1971). The effect of sample size is greatest when samples of relatively few individuals are dealt with. Although the present study did not use samples or subsamples of uniform size, the number of individuals was usually large, on the order of several hundred. They are, therefore, less likely to be subject to errors of the type that might be expected in smaller biological collections. For this reason it seems justifiable to accept the number of species observed in a sample as a measure of its richness.

The greater number of zooplankton species present in samples collected in oceanic waters as compared with coastal waters is well established (Raymont, 1963), and has been demonstrated for copepods by Cross (1964) and Bowman (1973). In the present study the number of species found in a single sample ranged from eight to 42. The mean number of shelf water species was significantly lower than means for slope and oceanic waters (Table 12). There was no significant difference in the number of species found in slope and oceanic waters.

Species Evenness. The other component which contributes to the diversity of communities is the measure of evenness, or the degree

to which species are equally distributed within a sample. This is sometimes discussed as equatibility, but that term is more properly restricted to the specific measure of evenness introduced by Lloyd and Gehlardi (1964). The measures of evenness used in the present study are derived from the frequently used Shannon-Weiner and Simpson indices of species diversity, together with two additional measures proposed and defined by Fager (1972) as measures of diversity and evenness. For all indices the values have been scaled so that a value of 1.0 represents maximum evenness possible within the system.

In all cases, the degree of evenness was greater in slope and oceanic waters than in shelf waters. Additionally, the magnitude of increase between shelf and slope or oceanic waters was similar for all of the indices, ranging from 1.13 to 1.33 times greater in slope or oceanic waters than in shelf waters.

The four indices yield different values for the degree of evenness present, however. Scaled values of the Simpson Index and Shannon-Weiner index gave much higher values of evenness than did the Standard Deviation or Number of Moves index. The former two indices show that the communities are from about 70 to 90 percent as even as possible, whereas the latter two show that the communities are only from about 58 to 77 percent and from 33 to 40 percent as even as possible, respectively. Fager (1972) has discussed the characteristics of these measures of evenness and pointed out the merits and deficiencies of each.

Although the use of indices such as those discussed above has been questioned, and they may have been misused in some instances,

the results of this study show that they are valuable tools which may be used to characterize communities. The detection of differences resulting from changes in species composition or relative abundance of the species comprising a community appears to be one of the greatest values of such indices.

SUMMARY

One hundred eighty zooplankton samples collected during August and November 1971 were examined. The distribution of total numbers of calanoid and non-calanoid copepods was determined. All mature copepods from 96 samples were identified and the abundance and distribution of each species was evaluated.

The copepod fauna observed in the present study is characteristic of the subtropical and temperate regions of the western Atlantic Ocean. One hundred one species were identified in the present study. Like total zooplankton biomass, the total number of copepods was greatest in shelf waters, less in slope waters and least in oceanic waters. This was more pronounced for calanoids than for non-calanoids.

Thirty-one species showed significantly different abundances among areas. Sixteen were more abundant in shelf waters and 15 were more abundant in slope or oceanic waters. Fifteen species exhibited significant diel differences in abundance. Of these, eight species were more abundant during daylight hours and seven were more abundant at night. The relative abundance of the most abundant species was different in the different areas.

Various measures of species diversity and its components were significantly different among the different areas. Diversity was greatest in oceanic waters, less in slope waters and least in waters over the continental shelf. The mean number of species present in

any single sample was greatest in oceanic and slope waters, and about 50 percent less in waters over the shelf. Species evenness was greatest in oceanic waters, less in slope waters and lowest in waters over the continental shelf. The various measures of diversity and its components may be considered to be valuable tools for detecting differences in zooplankton communities.

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EXAMINATION AND THESIS REPORT

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Major Field: Zoology

Title of Thesis: Zooplankton of the Gulf of Mexico:

Distribution of Displacement

Volumes, Occurrence of

Systematic Groups,

Abundance and Diversity

among Copepods.

Approved:

William B. Stickle Jr.

Major Professor and Chairman

James G. Traynham

Dean of the Graduate School

EXAMINING COMMITTEE:

W J Harman
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Date of Examination:

June 18, 1976